SCIRPUS AMERICANUS: ITS GROWTH CHARACTERISTICS AND VARIATION ON THE FRASER AND SKAGIT-STILLAGUAMISH ESTUARIES, SUMMER 1987

W. Sean Boyd

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Abstract

Biweekly surveys of Scirpus americanus growth were conducted on the Fraser and Skagit-Stillaguamish estuaries to determine differences within and between the two estuaries. A destructive sampling was undertaken at peak stem length to determine the relationships between growth indices and biomass. The three transects surveyed on the Fraser Estuary supported three distinct S. americanus communities, reflecting differences in key environmental factors. Those factors likely include salinity, tidal inundation/exposure ratio, and Snow Goose and swan grazing pressure. Compared to growth on the Fraser Estuary, S. americanus grew very poorly at the two transects on the Skagit-Stillaguamish Estuary. That poor growth could have been due to the relatively high Snow Goose grazing pressure and/or the high salinity there. Stem density explained most of the variance in above- and belowground plant biomass values in early August on the Fraser Estuary. To improve the relationships even further, destructive sampling at peak stem density should be undertaken.

Résumé

Les auteurs ont effectué des levés toutes les deux semaines dans les estuaires du Fraser et du complexe Skagit-Stillaguamish pour déterminer les différences dans le taux de croissance de Scirpus americanus d'un endroit à l'autre. Ils ont procédé à un échantillonnage destructif au moment où la tige des plantes atteignait une hauteur maximale pour établir des relations entre les indices de croissance et la biomasse. Le trois transects de l'estuaire du Fraser étaient caractérisés par les communautés distinctes de S. americanus, ce qui indique que les zones étaient soumises à des conditions environnementales différentes (notamment la salinité, l'exposition aux marées et le pâturage par des oies des neiges et des cygnes). Dans les deux transects établis dans l'estuaire du complexe Skagit-Stillaguamish, le taux de croissance de l'espèce étudiée était très faible. Cela pourrait être attribuable au pâturage relativement intense pratiqué par les oies des neiges ou à la forte salinité de l'eau, ou à ces deux facteurs à la fois. La densité des tiges expliquait la majeure partie des variations de la biomasse végétale dans l'estuaire du Fraser en août, tant au-dessus qu'au-dessous de la surface. Il faudrait effectuer des échantillonnages destructifs au moment où la densité des tiges atteint un sommet pour déterminer les relations avec plus de précision.

Table of Contents

	Page
Abstract	i
Resume	i
List of Figures	iii
List of Tables	iv
Acknowledgements	vi
1. Introduction	1
2. Methods	2
2.1 Data Collection	2
2.2 Data Analysis	3
3. Results	4
3.1 S. americanus Growth Patterns and Variation Between Transects on the Fraser Estuary	4
3.1.1 Aboveground Indices	4
Stem Density	4
Mean Stem Length	5
Maximum Stem Length	6
Relative Seed Abundance	6
Stem Mortality and Loss	6
Additional Plant Indices	7
3.1.2 Belowground Indices	7
Top Versus Bottom Subsamples	7
Differences Across Transects	8
3.1.3 Biomass and Ratios	8
3.1.4 Patchiness	8
3.1.5 Potential Growth	9
3.1.6 Differences Within Each Transect	10
3.2 Relationships Between Selected Indices and S. americanus Biomass	10
3.2.1 Aboveground Biomass	10
3.2.2 Belowground Biomass	11
3.3 Surface Salinities	11
4. Discussion	12
4.1 S. americanus Growth Variation on the Fraser Estuary	12
4.2 S. americanus Growth Variation Between the Fraser Estuary and the Skagit-Stillaguamish Estuary	14
4.3 Relationships Between S. americanus Growth Indices and Biomass	14
Literature Cited	15

List of Figures

		Page
1.	Fraser Estuary transects.	16
2.	Skagit-Stillaguamish Estuary transects.	17
3.	Stem density (live stems only) of Scirpus americanus on the Fraser Estuary 1987.	18
4.	Frequency histograms of (total) stem length of Scirpus americanus measured in the same non-random quadrats, Reifel Refuge transect 1987.	19
5.	Frequency histograms of (total) stem length of Scirpus americanus measured in the same non-random quadrats, Lulu Island transect 1987.	20
6.	Frequency histograms of (total) stem length of Scirpus americanus measured in the same non-random quadrats, Brunswick Point transect 1987.	21
7.	Mean (total) stem length of Scirpus americanus on the Fraser Estuary 1987.	22
8.	Maximum (total) stem length of Scirpus americanus on the Fraser Estuary 1987.	23
9.	Relative seed abundance of Scirpus americanus on the Fraser Estuary 1987.	24
10.	Stem density (live stems only) of Scirpus americanus on the Fraser Estuary 1987: random versus non-random quadrats	25
11.	Mean (total) stem length of Scirpus americanus on the Fraser Estuary 1987: random versus non-random quadrats	26
12.	Maximum (total) stem length of Scirpus americanus on the Fraser Estuary 1987: random versus non-random quadrats	27
13.	"Potential" stem density (number of live stems per quadrat; mean of five highest values) of Scirpus americanus on the Fraser Estuary 1987.	28
14.	"Potential" mean (total) stem length (mean of five highest values) of Scirpus americanus on the Fraser Estuary 1987.	29
15.	"Potential" maximum (total) stem length (mean of five highest values) of Scirpus americanus on the Fraser Estuary 1987.	30
16.	Scirpus americanus indices measured on the Fraser Estuary 1987: non-random quadrats only.	31
17.	Scatterplot showing the relationship between Scirpus americanus live rhizome biomass per core and stem density (live stems only) on the Fraser Estuary 1987	32
18.	Surface water salinities across the Fraser Estuary 1987	33

List of Tables

Page

1. Scirpus americanus stem density (no. stems quadrat^{-1}; live stems only; $\bar{x}\pm SE$) by transect, Fraser Estuary 1987. 34
2. Scirpus americanus growth indices ($\bar{x}\pm SE$), Skagit-Stillaguamish Estuary 1987. 35
3. Scirpus americanus mean stem length (cm; live stems only; $\bar{x}\pm SE$) by transect, Fraser Estuary 1987 36
4. Scirpus americanus maximum stem length (cm; live stems only; $\bar{x}\pm SE$) by transect, Fraser Estuary 1987 37
5. Scirpus americanus percentage of stems containing seedheads (%; live stems only; $\bar{x}\pm SE$) by transect, Fraser Estuary 1987 38
6. Scirpus americanus stem mortalities (no. dead stems quadrat^{-1} and percentage of live plus dead stems; $\bar{x}\pm SE$) by transect during surveys 6 and 7, Fraser Estuary 1987. (n=32 per transect for survey 6 and n=16 for survey 7; n=96 for the entire estuary for survey 6 and n=48 for survey 7.). 39
7. Scirpus americanus aboveground growth indices (live stems only; $\bar{x}\pm SE$) by transect during survey 7, Fraser Estuary 1987. (n=16 per transect; n=48 for the entire estuary). 40
8. Scirpus americanus belowground indices (g core^{-1}; $\bar{x}\pm SE$) for top and bottom core subsamples during survey 7, Fraser Estuary 1987. (n=96 for all indices). 41
9. Scirpus americanus belowground indices (g core^{-1}; $\bar{x}\pm SE$) for top and bottom core subsamples during survey 7, Reifel Refuge transect 1987. (n=32 for all indices) 42
10. Scirpus americanus belowground indices (g core^{-1}; $\bar{x}\pm SE$) for top and bottom core subsamples during survey 7, Lulu Island transect 1987. (n=32 for all indices). 43
11. Scirpus americanus belowground indices (g core^{-1}; $\bar{x}\pm SE$) for top and bottom core subsamples during survey 7, Brunswick Point transect 1987. (n=32 for all indices) 44
12. Scirpus americanus belowground indices (g core^{-1}; $\bar{x}\pm SE$) by transect during survey 7, Fraser Estuary 1987. The top and bottom core subsamples were added and the two cores per quadrat averaged. (n=16 per transect; n=48 for the entire estuary). 45
13. Scirpus americanus belowground indices (g core^{-1}; $\bar{x}\pm SE$) for bottom core subsamples by transect during survey 7, Fraser Estuary 1987. The two bottom core subsamples per quadrat were averaged. (n=16 per transect; n=48 for the entire estuary). 46
14. Scirpus americanus belowground indices (g core^{-1}; $\bar{x}\pm SE$) for top core subsamples by transect during survey 7, Fraser Estuary 1987. The two top core subsamples per quadrat were averaged. (n=16 per transect; n=48 for the entire estuary). 47
15. Scirpus americanus biomass and ratio values ($\bar{x}\pm SE$) by transect during survey 7, Fraser Estuary 1987. (n=16 per transect; n=48 for the entire estuary) 48
16. Scirpus americanus stem density, mean stem length, and maximum stem length (live stems only; $\bar{x}\pm SE$) by transect, Fraser Estuary 1987. All data were collected from non-random quadrats (see text) 49

List of Tables (cont'd)

Page

17. Highest stem density, mean stem length, and maximum stem length values recorded for Scirpus americanus by transect, Fraser Estuary 1987. ($\bar{x}\pm$SE of five highest values (maximum value in brackets); n=16 for surveys 1 and 7; n=24 for surveys 2 through 6). 50
18. Summary of highest values recorded for selected Scirpus americanus growth indices by transect during survey 7, Fraser Estuary 1987. ($\bar{x}\pm$SE of five highest values (maximum value in brackets); n=16 per transect). Aboveground indices are for live stems only 51
19. Correlations between Scirpus americanus growth indices during survey 7, Fraser Estuary 1987. (Pearson correlation coefficient; probability; n=48 for all indices). 52
20. Correlations between Scirpus americanus aboveground biomass values and growth indices during survey 7, Fraser Estuary 1987. (Pearson correlation coefficient; probability; n=48 for all indices) 53
21. Multiple regression analysis results of Scirpus americanus aboveground biomass against growth indices, Fraser Estuary 1987. (survey 7; n=16 per transect; n=48 for the entire estuary). 54
22. Multiple regression analysis results of Scirpus americanus aboveground biomass against stem density and mean stem length (live portion; cubed), Fraser Estuary 1987. (survey 7; n=16 per transect; n=48 for the entire estuary). 55
23. Multiple regression analysis results of Scirpus americanus mean stem biomass against growth indices, Fraser Estuary 1987. (survey 7; n=16 per transect; n=48 for the entire estuary). 56
24. Multiple regression analysis results of Scirpus americanus mean stem biomass against mean stem length (live portion; cubed) and stem basal diameter, Fraser Estuary 1987. (survey 7; n=16 per transect; n=48 for the entire estuary). 57
25. Correlations between Scirpus americanus belowground biomass values and growth indices during survey 7, Fraser Estuary 1987. (Pearson correlation coefficient; probability; n=48 for all indices) 58
26. Multiple regression analysis results of Scirpus americanus belowground biomass against growth indices, Fraser Estuary 1987. (survey 7; n=16 per transect; n=48 for the entire estuary). 59
27. Multiple regression analysis results of Scirpus americanus belowground biomass against stem density, Fraser Estuary 1987. (survey 7; n=16 per transect; n=48 for the entire estuary). 60
28. Surface water salinities (ppt; $\bar{x}\pm$SE(n)) by transect, Fraser Estuary 1987. 61

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1. Introduction

A relatively large population of Lesser Snow Geese (Anser caerulescens caerulescens) winters on the Puget Trough, alternating between the Fraser Estuary (British Columbia) and the Skagit-Stillaguamish Estuary (Washington) from early October to late April. The geese graze heavily on the rhizomes of three-square bulrush (Scirpus americanus Pers.), a brackish marsh species that grows in large homogeneous stands on both estuaries. In recent years, both the peak number of Snow Geese and the number of Snow Goose-days experienced by the two estuaries have increased considerably (Boyd, unpublished data).

High concentrations of wintering geese can have profound effects on the structure and composition of marsh communities (Lynch et al. 1947, Smith and Odum 1981, Smith 1983, Giroux 1986). If a marsh's food reserves are depleted to the extent that carrying capacity is exceeded, the geese are forced to disperse to other locations, including suitable farmland if present. The marsh on the Skagit-Stillaguamish Estuary has probably been under considerable grazing pressure for years. Snow Goose numbers have historically been much higher there than on the Fraser Estuary (Jeffrey and Kaiser 1979). Also, the geese have utilized farmland on the Skagit-Stillaguamish Estuary to a much greater extent, especially from mid-December to late April. The marsh located at the George C. Reifel Bird Sanctuary on the Fraser Estuary is of concern because Snow Geese have concentrated there in high numbers during past hunting seasons, particularly in the early years after the establishment of the sanctuary in 1963 (Robert Husband and Russell Young, pers. comm.). Since about 1980, the geese have also fed extensively on farmland located at and adjacent to the Alaksen National Wildlife Area on Westham Island; they have apparently reduced their use of the Westham Island foreshore at the same time.

The above scenario, especially the perceived recent switch from foreshore to field use by Snow Geese, raises questions about the state of the marsh on the Fraser Estuary foreshore. To what extent have the geese impacted the S. americanus community? What is that community's carrying capacity? What are the consequences of an increasing goose population?

To date, only one study of Snow Goose use of the Fraser Estuary has been conducted (Burton 1977). That study involved a small population of geese and only assessed changes in S. americanus root and rhizome biomass over one winter. I am proposing to undertake a longer-term investigation. Exclosures will be used over several years to determine grazing rates, plant regeneration rates, maximum potential biomass values, environmental influences on plant growth, etc. Plant growth will be monitored at precisely the same locations (i.e. the same quadrats) from one year to the next; hence, a non-destructive sampling technique is required so that the plants are not disturbed. Giroux (1986) used such a technique in his study of Greater Snow Goose utilization of marshes on the St. Lawrence Estuary. The technique requires that the relationships (i.e. regression equations) between aboveground plant growth indices and biomass be established. Once known, only those indices that are capable of predicting biomass need to be measured. The technique also allows for greater sample sizes compared to destructive sampling since it is not nearly as time-consuming.

The present study was undertaken to develop the above relationships. In addition, data were collected to describe growth curves and to determine the variability of S. americanus growth indices and above- and belowground biomass within and between the Fraser and Skagit-Stillaguamish estuaries. S. americanus is the focus of attention because of its importance as the preferred food of Snow Geese. Also, because its distribution and that of the wintering geese coincide, S. americanus may be a good indicator of the impact Snow Geese are having on the entire foreshore marsh and its associated plant communities.

2. Methods

2.1 Data Collection

Three transects were established through pure stands of S. americanus on the Fraser Estuary (Figure 1). The Reifel Refuge and Brunswick Point transects were aligned in a southwest to northeast direction, almost perpendicular to the dyke, whereas the Lulu Island transect was aligned north to south, parallel to the dyke. Those alignments reflect the width of the S. americanus zone at each transect.

Eight semi-permanent plots, divided into four pairs, were delineated with wooden stakes along each transect with approximately 50 m intervals between pairs. The dimensions of each transect were approximately 150 m (long) by 25 m (wide). Surveys were conducted every two weeks to coincide with daylight low tide cycles from mid-May to early August 1987. During surveys 2 to 6, three randomly selected, 25 cm by 25 cm quadrats were sampled non-destructively at each plot for a total of 24 quadrats per transect. Each quadrat was located using a combination of two "over-the-shoulder" tosses of a pencil. The quadrats were generally within 10 m of their associated plot markers. The following plant data were collected from each quadrat: number of live and dead stems; mean total (i.e. live plus dead portion) length of 10 random, live stems; maximum total stem length; and the number of stems supporting seedheads. If less than 10 stems were present in a quadrat, stems closest to it were measured for length. A stem was considered dead if it lacked any green colour. Also, residual surface water salinity was measured from depressions in the marsh platform, using a hand-held refractometer.

During the first survey, only two random quadrats per plot were sampled, as above. During the last (or seventh) survey, two random quadrats per plot were sampled using a destructive technique; that is, all aboveground plant material was clipped at the substrate surface and two 12.5 cm diameter by 30 cm long substrate cores were excavated. The cores were located diagonally adjacent to one another. They were taken using a metal pipe serrated at its cutting edge. A 30 cm core length was used because it held more than 95% of the total live rhizome biomass during a previous sampling effort (unpublished data). Also, except for considerable root biomass at Lulu Island and some root and rhizome biomass within high stem density zones at Reifel Refuge, little belowground plant material was present below 30 cm in the majority of core holes excavated during survey 7.

The above samples were frozen until they could be processed. At that time, the aboveground material was sorted into live and dead stems and each live stem was measured for basal diameter, live portion length, and total length (live plus dead portions). All stems were thoroughly washed, dried in a forced-air oven for 24 hours at 100°C, and weighed to the nearest 0.001 g. The belowground material was split into top 15 cm and bottom 15 cm subsamples, hand-massaged and spray-rinsed over a 0.5 mm mesh screen, sorted into live and dead rhizomes, roots, and miscellaneous plant material, and then dried and weighed as above. Final results for aboveground biomass values were expressed on g quadrat^{-1} and g m^{-2} bases. Belowground biomass values were expressed on g core^{-1} and g m^{-2} bases.

Timing for the destructive sampling was planned to coincide with peak stem length, since it was thought to be a reasonably good point on the growth curve at which to determine the relationships between growth indices and biomass. After each survey, mean and maximum stem lengths were plotted against date. When it appeared that peak lengths were being approached, a decision was made to proceed with the destructive technique during the next daylight low tide cycle (survey 7).

Although the above quadrats at each semi-permanent plot were located randomly, the plot markers themselves were not. They were arranged in relatively straight lines about 50 m apart for ease of relocating them during peak growth. Their exact positioning was biased away from features such as depressions, channels, and hummocks. During surveys 1 and 7, non-destructive plant data were collected from two quadrats positioned side-by-side at each plot marker. During surveys 2 to 6, only one of those quadrats per plot (consistently the same one) was used. The resulting data on individual stem lengths were used to help evaluate changes in stem density by plotting frequency histograms. Also, plant growth in the adjacent quadrats were compared between survey 1 and survey 7 to assess handling effects (i.e. the impact of measuring the same plots every two weeks). Finally, the non-random plant data were compared with the randomly collected data to assess potential growth and patchiness at each transect. Wire mat exclosures (1.25 x 2.5 m; mesh size=5 x 5 cm) were placed flat over the non-random plots in September 1987; the plots will be monitored annually to determine the maximum potential growth of S. americanus without the direct effect of goose or swan grazing on rhizome material.

The non-destructive sampling technique was conducted along two transects on two different dates in the Skagit-Stillaguamish Estuary (Figure 2). Each transect contained eight plots, grouped in pairs approximately 50 m apart, except the north transect during the first survey which contained 12 plots. Four random quadrats were sampled at each plot.

2.2 Data Analysis

The S. americanus data were summarized by the entire Fraser Estuary (i.e. all transect data pooled) and by individual transect. Aboveground growth indices were plotted against date to describe changes over the growing season. Non-parametric (Kruskall-Wallis) One-way ANOVAs in conjunction with non-parametric multiple range tests were used to determine statistical differences between transects for the aboveground indices. Parametric Paired-sample T tests and One-way ANOVAs were used to determine the differences in

belowground indices between the top and bottom core subsamples and differences between transects, respectively. Multiple regression analysis was used to determine the relationships between selected growth indices and above- and belowground biomass. The Statistical Package for Social Sciences (SPSS:X) was used for most of the above analyses. A significance level of 5% was chosen prior to analyses.

3. Results

Because this report is largely "descriptive" in nature, some repetition was necessary in the presentation of the results. Most of the information, including the means, standard errors, sample sizes, and results of statistical tests, are presented in the tables. The figures summarize the data for the Fraser Estuary and show differences in mean values between transects.

3.1 S. americanus Growth Patterns and Variation Between Transects on the Fraser Estuary

3.1.1 Aboveground Indices

Stem Density

With respect to the entire Fraser Estuary (i.e. all transect data pooled), S. americanus stem density (live stems only) increased steadily throughout the summer, from 35.0 stems quadrat^{-1} (562 stems m^{-2}) on 13-19 May, to a high of 61.2 stems quadrat^{-1} (979 stems m^{-2}) on 7-9 July (Figure 3; Table 1). Density then declined by 41% to 36.2 stems quadrat^{-1} (579 stems m^{-2}) by the last survey, 5-7 August. The maximum rate of increase (0.9 stems quadrat^{-1} day^{-1} (14 stems m^{-2} day^{-1})) occurred between 22-24 June and 7-9 July. The maximum rate of decrease (1.1 stems quadrat^{-1} day^{-1} (17 stems m^{-2} day^{-1})) occurred between 21-23 July and 5-7 August.

Stem density at each transect varied similarly (Figure 3; Table 1). Peaks were reached on or near 7-9 July and declines occurred soon after. No discrete eruptions of new shoots were apparent over the summer. After the main cohort of stems initiated growth in early May, new stems were added at a relatively low but constant rate until 7-9 July. That is clearly demonstrated by the frequency histogram plots of individual stem lengths measured in the non-random quadrats (Figures 4 to 6). Those same quadrats (n=8 per transect) were sampled every two weeks. Reifel Refuge and Brunswick Point had approximately 2% new stems (<10 cm) in surveys 3 through 5, 8-10 June to 7-9 July. Lulu Island had higher proportions of new stems during those surveys (about 10%). Reifel Refuge and Brunswick Point had no or very few new stems after 7-9 July, whereas Lulu Island supported higher numbers of new stems until 5-7 August. The declines in stem density (25, 44, and 51% from 7-9 July to 5-7 August for Reifel Refuge, Lulu Island, and Brunswick Point, respectively) were due to the loss or burial of older stems (discussed below).

Brunswick Point experienced the highest rates of increase and decrease in stem density (1.5 and 1.5 stems quadrat^{-1} day^{-1} (or 24 and 24 stems m^{-2} day^{-1}), respectively) followed by Lulu Island (0.9 and 1.2 (or 14 and 19), respectively). Reifel Refuge had the lowest rates (0.5 and 0.5 (or 8 and 8), respectively). The highest rates of increase for Brunswick Point and Lulu

Island were achieved between 23-24 June and 8-9 July whereas for Reifel Refuge it occurred earlier, between 8 June and 22 June.

Although there was a trend of highest stem densities at Lulu Island throughout the summer, the non-parametric One-way ANOVA suggested only two differences across transects at the 5% level of significance ($P<0.010$ and $P<0.050$ for surveys 2 and 4, respectively; Table 1). Stem densities were similar for all other surveys.

The transects on the Skagit-Stillaguamish Estuary had S. americanus stem densities that were considerably lower than those reported above (Table 2). Transect A reached only 3.3% whereas transect B reached 41.9% of the overall values for the Fraser Estuary during survey 6, 21-23 July.

Mean Stem Length

Over the entire Fraser Estuary, S. americanus mean stem length (live stems only; total length) increased from 10.2 cm on 13-19 May to 59.1 cm on 21-23 July and then declined to 55.7 cm by 5-7 August (Figure 7; Table 3). The maximum rate of increase (1.2 cm day^{-1}) occurred between 8-10 June and 22-24 June.

Growth curves were clearly different for the three transects (Figure 7; Table 3). Lulu Island had much lower stem lengths than the other transects throughout the summer, except during the last survey, 5-7 August. Its highest rate of stem growth was 0.7 cm day^{-1}, occurring between 9 June and 23 June. That coincided with the same period of maximum stem growth for the other transects, however Brunswick Point reached 1.2 cm day^{-1} and Reifel Refuge attained 1.5 cm day^{-1}, rates that were 1.7 and 2.2 times greater than that at Lulu Island, respectively.

Brunswick Point and Reifel Refuge had similar growth patterns until 8-10 June after which they diverged considerably, with Reifel Refuge attaining higher mean stem lengths for the remainder of the survey period. All transects appeared to reach peak stem length by 5-7 August and possibly even by 21-23 July.

The above trends were supported by the non-parametric One-way ANOVA (Table 3). From 25-27 May to 21-23 July, Lulu Island mean stem length was less than that for the other transects ($P<0.001$). Reifel Refuge experienced a greater mean stem length than Brunswick Point from 7-9 July to 5-7 August ($P<0.001$). One apparent anomaly was the considerable decrease in mean stem length at Brunswick Point from 21-23 July to 5-7 August (discussed below).

Data collected from the two transects on the Skagit-Stillaguamish Estuary (Table 2), particularly from transect B, suggested a similar S. americanus growth pattern to the Fraser Estuary Lulu Island transect. Transect A achieved an even lower mean stem length.

Maximum Stem Length

Maximum and mean S. americanus stem lengths (live stems only; total lengths) were highly correlated for the non-destructive samples (Pearson correlation coefficient R=0.936; P<0.001; n=408) and for the destructive samples (R=0.968; P<0.001; n=48). It is not surprising, therefore, that those two stem length parameters followed the same pattern and experienced the same relative variability for both the Fraser and Skagit-Stillaguamish estuaries (Figure 8; Table 4).

Relative Seed Abundance

The percentage of S. americanus stems containing seedheads (live stems only) increased from 4.4% during 13-19 May to a peak of 32.5% during 7-9 July and then declined to 24.9% by 5-7 August, on an entire estuary basis (Figure 9; Table 5). The increase corresponded to stem growth and maturation whereas the decrease was associated with the senescence and loss or burial of older, seed-bearing stems from the standing crop.

On an individual transect basis, Lulu Island tended to have a lower percentage of stems containing seeds but the differences were (generally) not significant at the 5% level (Figure 9; Table 5). Survey 6, 21-23 July, was the only occasion in which Lulu Island was different (from Reifel Refuge) (P<0.050).

Stem Mortality and Loss

The number of dead S. americanus stems recorded per quadrat increased from nil or very few during the first five surveys (13-19 May to 7-9 July) to 4.3 (69 stems m^{-2}) by survey 7 (5-7 August), on an estuary-wide basis (Table 6). For survey 7, that represented 5.6% of the total number of live plus dead stems present. Mortalities of 1.7, 5.4, and 5.7 stems $quadrat^{-1}$ (27, 86, and 91 stems m^{-2}) were recorded during survey 7 at Reifel Refuge, Lulu Island, and Brunswick Point, respectively (Table 6). Those numbers corresponded to 3.2, 6.9, and 6.8% of the total number of live plus dead stems present at each transect. The above percentages, in turn, were small compared to the declines already noted in stem densities from 7-9 July to 5-7 August. It appears that, even before reaching peak length, stems began their senescent phase (from the top down). Once nearly or completely without green growth, they were broken by tide and wave action and many were subsequently buried or washed out of the marsh altogether.

The loss of stems at Brunswick Point by survey 7 deserves special attention. During that survey, mats of filamentous algae were observed to cover large areas of the transect. The algae held back receding tidal water, thereby submerging and water-logging the S. americanus stems, causing them to become brittle and easily broken. That observation was substantiated by a comparison of the proportion of broken stems counted during processing for the destructive technique. Brunswick Point had 13.3% broken stems whereas Reifel Refuge had only 6.5% and Lulu Island 9.2%. Therefore, not only did Brunswick Point have proportionally more stems lost from the system than the other transects by survey 7, it also had stems missing proportionally more length.

Mats of algae in combination with salinity stress could have caused those differences at Brunswick Point.

Reifel Refuge had fewer stem mortalities than the other transects on both survey 6 ($P<0.001$) and survey 7 ($P<0.001$) (Table 6). Its mortalities were only 21 and 16% of those encountered during 21-23 July and only 32 and 30% of those during 5-7 August at Lulu Island and Brunswick Point, respectively.

Those transect differences were reflected in the stem density declines between 7-9 July and 5-7 August.

Additional Plant Indices

During the last survey, Reifel Refuge was different from the other transects for seven of ten indices and it was different from Brunswick Point for two of the remaining three indices (Table 7). In fact, S. americanus stems growing at Reifel Refuge were longer ($P<0.001$), had greater basal diameters ($P<0.001$), and were (therefore) heavier ($P<0.001$) than stems growing at the other transects. Stem biomass (live and total) was also higher at Reifel Refuge but the difference was only significant with respect to Lulu Island ($P<0.025$). Stem density was the only index not different across transects ($P>0.250$).

Results for the last survey (5-7 August) at Brunswick Point must be interpreted with caution. As noted, that transect experienced reduced stem densities and stem lengths at that time which were out of character in terms of the previous six surveys.

3.1.2 Belowground Indices

Top Versus Bottom Subsamples

With respect to the entire Fraser Estuary (i.e. all transects amalgamated), all S. americanus belowground indices, except live and total rhizome biomass, were greater in the top core subsamples ($P<0.001$) (Table 8). Except for total rhizomes plus roots, the same top-bottom differences were apparent at Reifel Refuge and Brunswick Point (Tables 9 to 11). The top core subsamples had greater biomass values for all indices, including live and total rhizomes ($P=0.004$ and $P=0.019$, respectively), at Lulu Island.

The top and bottom core subsamples were fairly highly correlated ($R=0.759$; $P<0.001$; $n=96$), in spite of the fact that the top subsamples would have been under proportionally more grazing pressure from geese and swans. Also, the difference between top and bottom cores with respect to rhizome biomass would likely have been significant in the absence of grazing; in other words, potential rhizome biomass is probably higher in the top 15 cm substrate layer.

Differences Across Transects

When the top and bottom core subsamples were added and the two cores per quadrat averaged (Table 12), live rhizome biomass did not vary ($P=0.861$) from transect to transect ($\bar{x}=2.589$, 2.165 and 2.378 g core^{-1} for Reifel Refuge, Lulu Island, and Brunswick Point, respectively). Root biomass at Lulu Island ($\bar{x}=10.764$ g core^{-1}) and at Reifel Refuge ($\bar{x}=8.274$g core^{-1}) were higher ($P<0.001$) than at Brunswick Point ($\bar{x}=4.632$ g core^{-1}). Similarly, total rhizome plus root biomass and total belowground plant biomass were highest at Lulu Island followed by Reifel Refuge and then Brunswick Point; only Lulu Island and Brunswick Point were different ($P=0.011$ and $P=0.014$, respectively), however.

The bottom core subsamples (averaged for each quadrat) varied across transects in exactly the same manner as above, the only difference being the magnitude of the indices (Table 13). The top core subsamples varied similarly with the exception of root biomass (Table 14). The three transects had different root biomass values ($P<0.001$), again with Lulu Island having the highest value followed by Reifel Refuge and then Brunswick Point.

3.1.3 Biomass and Ratios

As noted, differences existed between transects with respect to above- and belowground biomass during 5-7 August (Table 15). For the former, Reifel Refuge had higher values than only Brunswick Point ($P<0.025$). For the latter, Lulu Island had higher values than only Brunswick Point ($P<0.025$). Despite those differences, however, total biomass did not vary from transect to transect ($P>0.050$). Lulu Island had the highest total biomass ($\bar{x}=1256$ g m^{-2}) followed closely by Reifel Refuge ($\bar{x}=1181$ g m^{-2}) and then Brunswick Point ($\bar{x}=768$ g m^{-2}).

Aboveground biomass was not highly correlated with belowground biomass ($R=0.539$; $P<0.001$; $n=48$) or root biomass ($R=0.367$; $P=0.010$; $n=48$) but it was relatively highly correlated with live rhizome biomass ($R=0.726$; $P<0.001$; $n=48$). The ratio of above- to belowground biomass was higher ($P<0.001$) at Reifel Refuge ($\bar{x}=0.284$) than at Lulu Island ($\bar{x}=0.122$) and Brunswick Point ($\bar{x}=0.195$). The same differences were apparent for the ratio of aboveground biomass to live rhizome biomass ($P<0.005$). Those differences were probably due more to the higher aboveground biomass at Reifel Refuge rather than to its belowground biomass.

3.1.4 Patchiness

Brunswick Point was observed to have a "patchier" environment than the other transects. Its platform was pitted by depressions of various sizes and depths in which vegetation was completely absent (recent Snow Goose or swan feeding craters) or sparse (older, regenerating craters). Those craters were often adjacent to very lush, dense clumps of *S. americanus*. By contrast, the plant communities at Lulu Island and Reifel Refuge were much more uniform in appearance.

The above observations were substantiated by a comparison of the coefficients of variation (CV) of almost all plant indices (except percentage of stems with seedheads and stem mortalities which are independent of topography). The most obvious index, stem density CV, was higher at Brunswick Point than at the other transects throughout the entire summer. At peak density (7-9 July), Brunswick Point's stem density CV was 88.5% compared to 66.1% at Reifel Refuge and only 48.8% at Lulu Island. During the final survey (5-7 August), stem density CV was 108.0% at Brunswick Point, 55.9% at Reifel Refuge, and 59.6% at Lulu Island.

Stems growing in craters were submerged under 5-10 cm of standing water at low tide. They usually grew with little vigour compared to stems on the higher, drier portions of the marsh platform. As a result, stem length and basal diameter CVs increased with the number and distribution of craters present. Mean stem length CV was higher at Brunswick Point than at the other transects throughout the summer. During the last survey (5-7 August), mean stem length CV was 44.6% at Brunswick Point, 13.5% at Reifel Refuge, and 13.9% at Lulu Island. Maximum stem length CV followed the same pattern. Also during the last survey, stem basal diameter CV was 38.7% at Brunswick Point, 9.5% at Reifel Refuge, and 12.9% at Lulu Island.

Similar differences between transects were present with respect to above- and belowground biomass values. During the last survey, live stem biomass CV was 128.3% at Brunswick Point, 61.4% at Reifel Refuge, and 59.4% at Lulu Island; live rhizome biomass CV was 122.5% at Brunswick Point, 70.1% at Reifel Refuge, and 74.6% at Lulu Island; finally, root biomass CV was 73.9% at Brunswick Point, 48.8% at Reifel Refuge, and 43.2% at Lulu Island.

A comparison of the plant data collected in the random versus the non-random quadrats also substantiated the greater degree of patchiness at Brunswick Point (Figures 10 to 12; Table 16). Not only were stem density and stem length values greater in the non-random quadrats (a result of plot location selection away from topographic irregularities), the differences between the random and non-random quadrats were much greater at Brunswick Point than at the other transects.

3.1.5 Potential Growth

Results presented above represented current, mean values for each transect based on at least 16 quadrats and, during most surveys, 24 quadrats. As indicated, the "patchier" the plant growth at each transect, the higher the variability for some indices and consequently the lower their mean values. The highest values achieved, on the other hand, would have been more representative of the growth potential of S. americanus at each transect. Both the maximum value and mean of the five highest values (the number five was arbitrarily chosen) suggested that Brunswick Point had a potential stem density that was at least as great as, if not greater than, that at Reifel Refuge and Lulu Island (Figure 13; Table 17). Of the seven surveys, Brunswick Point had the highest maximum values for five surveys and the highest mean top five values for six surveys, results that were very different from the overall mean values presented earlier (Figure 3; Table 1).

Potential mean and maximum stem lengths varied across transects throughout the summer in roughly the same manner as actual stem lengths (Figures 14 and 15; Table 17). Reifel Refuge had the highest maximum values and mean top five values of stem lengths, Lulu Island had the lowest, and Brunswick Point had values somewhere between those two. That trend was consistent for all other aboveground indices during survey 7 (Table 18): maximum stem length, mean stem basal diameter, stem biomass per quadrat, and mean stem biomass. Rhizome biomass and root biomass did not fit the same trend, however.

The greater potential stem density at Brunswick Point was also substantiated by an analysis of the data collected in the non-random quadrats (Figure 16). Brunswick Point had the highest stem density values, Reifel Refuge had the lowest values, and Lulu Island had values between those two on all surveys. Plots of stem length data collected in the non-random quadrats (Figure 16) were similar to those for the potential values presented above.

3.1.6 Differences Within Each Transect

One-way ANOVAs for each of the major S. americanus above- and belowground indices measured during survey 7 suggested that there were no differences between plots within each transect ($P>0.050$ in all cases). Also, when ranked, there were no obvious trends in any of the indices from high marsh (i.e. plots nearest the dyke) to low marsh (i.e. plots furthest from the dyke) for the Reifel Refuge and Brunswick Point transects. The transect at Lulu Island was not considered in that last respect because it ran parallel to the dyke.

3.2 Relationships Between Selected Indices and S. americanus Biomass

3.2.1 Aboveground Biomass

As expected, many of the growth indices and biomass values discussed above were positively correlated (Tables 19 and 20). However, stepwise regression analysis showed that stem density was clearly the best predictor of S. americanus aboveground biomass, both live and total (live plus dead) stem biomass (Table 21). Stem density was the first variable entered into the regression equations in all cases. Various forms of mean stem length were next in importance, however mean stem length (live portion) cubed was the most consistent variable. That last variable was used because, of all the different variables and different powers of those variables tested (aside from stem density), it produced the highest correlation coefficient with stem biomass.

For consistency, regressions were run again using only stem density and mean stem length (live portion) cubed as independent variables (Table 22). Except for total stem biomass at Lulu Island, both variables were consistently entered into the final regression equations and they explained a total of 91% of the variance in both Fraser Estuary live and total stem biomass ($P<0.0001$). By transect, they explained from 93 to 96% of live stem biomass and from 91 to 98% of total stem biomass ($P<0.0001$ in both instances). Reifel Refuge experienced the highest unexplained variance (residual standard error) whereas Lulu Island had the lowest for both biomass values.

In a related set of regressions, mean stem length (live portion) cubed and stem basal diameter were the best predictors of mean stem biomass (Tables 23 and 24). Those variables explained a total of 91% of the variance in both Fraser Estuary mean live and mean total stem biomass ($P<0.0001$). By transect, they explained from 80 to 97% of the mean live stem biomass and from 75 to 90% of the mean total stem biomass ($P<0.0001$ in both instances). Again, the highest unexplained variance was at Reifel Refuge whereas the lowest was at Lulu Island for both biomass values.

3.2.2 Belowground Biomass

As with aboveground biomass, a number of positive correlations existed between plant indices and belowground biomass values (Table 25). Few indices other than stem density, however, were good, consistent predictors of live rhizome, root, and total belowground biomass (Table 26). When regressed alone, stem density accounted for 77% of the Fraser Estuary live rhizome biomass ($P<0.0001$) and, by transect, from 73 to 90% ($P<0.0001$) (Figure 17; Table 27). Brunswick Point experienced the highest unexplained variance whereas Reifel Refuge had the lowest. Regression lines describing the relationship between live rhizome biomass and stem density were not different across transects ($P=0.170$).

When analysed separately, live rhizome biomass in the top core subsamples (i.e. the two subsamples averaged per quadrat) was correlated higher with stem density ($R=0.921$; $P<0.0001$; $n=48$) than was rhizome biomass in the bottom core subsamples ($R=0.772$; $P<0.0001$; $n=48$) or in the entire core (i.e. the top and bottom subsamples added and the two cores averaged per quadrat; $R=0.875$; $P<0.001$; $n=48$) over the entire estuary. Those differences may be explained by the fact that the top subsamples had 15% greater rhizome biomass than the bottom subsamples (again, almost different at the 5% level; $P=0.057$) and the upper substrate was therefore supporting proportionally more stems.

Stem density did not account for nearly as much of the variance in root biomass or total belowground biomass as it did for rhizome biomass.

3.3 Surface Salinities

The effect of the Fraser River freshet was apparent on the surface water salinities during 22-24 June (Figure 18; Table 28). Overall salinities decreased to 3.3 ppt at that time from 8.9 ppt during 25-27 May. They then increased to a high of 12.8 ppt during 21-23 July. Reifel Refuge had lower salinities than the other transects throughout the summer ($P<0.025$). Salt water influence was totally absent at Reifel Refuge from 8-10 June to 7-9 July, the period of maximum *S. americanus* stem length and stem density growth rates.

4. Discussion

4.1 S. americanus Growth Variation on the Fraser Estuary

Abiotic factors, such as substrate salinity and tidal exposure/inundation ratio, influence the distribution of marsh plant species on estuaries (Chapman 1960, Eilers 1975, Hutchinson 1982, Dawe and White 1982). Those factors also tend to set the maximum or potential limits to growth. Biotic factors, such as goose and swan grazing, can reduce growth to a level below its potential. The data collected in this study strongly suggest that both the potential and actual growth of S. americanus are location-specific: the transects surveyed supported three distinct growth forms, no doubt due to the influence of three distinct abiotic and biotic environments.

Regarding potential growth of aboveground indices, Reifel Refuge had the highest mean and maximum stem lengths, stem basal diameter, mean stem biomass (hence the highest stem vigour), and aboveground biomass. Lulu Island, at the other extreme, had the lowest values for those same indices and Brunswick Point had values somewhere between. With respect to actual growth, the same between-transect differences were apparent. One important difference between potential and actual growth of S. americanus involved stem density: Brunswick Point had potential densities that were as great as, or greater than, those at the other transects whereas its actual densities were (generally) less than those at the other transects throughout the summer.

With regard to potential growth of belowground material, Lulu Island had the lowest live rhizome biomass but the highest root biomass (in fact, it supported almost twice as much root biomass as Brunswick Point). The actual growth data showed the same trend for root biomass but rhizome biomass did not differ across transects.

Another important difference between transects was the degree of patchiness. Brunswick Point had consistently the greatest coefficients of variation for all indices, substantiating ground and air observations that the platform there was extremely patchy. That high variability, in turn, affected the mean or actual values of all indices calculated for that transect.

Surface water salinity was the only abiotic factor measured. Reifel Refuge had lower salinities than the other transects throughout the summer. During the initial growth phase of S. americanus, in which high salt concentrations can have negative effects (Eilers 1975), surface salinities were between zero and 5 ppt at Reifel Refuge, between 5 and 8 ppt at Brunswick Point and around 14 ppt at Lulu Island. The "fresher" water environment at Reifel Refuge could have been a key factor in the high vigour of S. americanus stems growing there.

As noted in the introduction, Snow Geese have concentrated to high numbers at the Reifel Refuge foreshore since its establishment in 1963, especially during the 1960's and 1970's and especially in daylight hours during the hunting season. Their heavy grazing pressure likely resulted in the uniform, low elevation topography at that transect. That topography probably influenced substrate salinities and the tidal exposure/inundation ratio and therefore, indirectly, the growth of S. americanus. That, along with a lower intensity of grazing in recent years, could have resulted in a more optimum rhizome and stem spacing which, in turn, could have been

responsible for the high stem vigour and high biomass of S. americanus there. The above is speculation only. Further study, involving additional transects, is needed to determine if the transect monitored in this study is truly representative of the entire S. americanus community at Reifel Refuge.

The phenotypic differences recorded for S. americanus over fairly distant transects in this study have also been measured over a much shorter distance at Sea Island (Figure 1). There, Karagatzides (1987) found S. americanus to have significantly greater shoot densities and above- and belowground biomasses in the "upper" marsh compared to a site less than 250 m away but lower in elevation. He concluded that the high and low S. americanus represented ecophenes or plastic growth forms which were responding to local environmental conditions.

Stem density and rhizome (live plus dead) biomass measured by Karagatzides (1987) were much greater at Sea Island (approximately 1500 and 3600 stems m^{-2} and 400 and 1100 g m^{-2} for lower and upper marsh, respectively, for July/August) than at Reifel Refuge, Lulu Island, and Brunswick Point (approximately 800, 1125, and 1000 stems m^{-2} and 210, 200 and 200 g m^{-2}, respectively, for early August in this study). Root biomass values between study sites, however, were more similar (approximately 300 and 1100 g m^{-2} for lower and upper marsh at Sea Island, respectively, and about 675, 875, and 375 g m^{-2} at Reifel Refuge, Lulu Island and Brunswick Point, respectively, in this study). The high stem density and rhizome biomass measured by Karagatzides may be due to the fact that he used only five quadrats sampled in a non-random fashion.

Burton (1977) found mid-winter S. americanus rhizome standing crop to vary considerably between transects on the Fraser Estuary. His Reifel Refuge transect had lower rhizome biomass than did his Brunswick Point transect and both of those were lower than his Williams Road transect (Burton's transects were close to those used in this study). Giroux (1986), working on the St. Lawrence Estuary, also found major differences in S. americanus above- and belowground biomass between four adjacent plant communities.

The relative location differences documented in the above studies and in this study strongly suggest that S. americanus growth variability seems to be the rule rather than the exception. That variability has the following repercussions: (1) Caution should be exercised when extrapolating growth data for S. americanus and other marsh plant species from one location to another, even over short distances. The abiotic and biotic environments could be very different between locations resulting in different actual and potential plant growth. That appears to be true between estuaries, across the Fraser Estuary, and perhaps even over small distances within the Fraser Estuary (e.g. Reifel Refuge). (2) Caution should be exercised when pooling transect data to determine overall average biomass values for the Fraser Estuary. As many transects as possible should be established and overall estuarine values calculated through weighting by the areal extent represented by each transect. (3) To gain a better appreciation of the maximum growth potential at any location, and thereby determine the impact of Snow Geese and swans, exclosures should be used to prevent grazing. Important abiotic factors could be monitored along with the major plant growth indices throughout the growing season and over several years. Such a monitoring scheme would also help determine the effects of climate and Fraser River freshet (i.e. annual variation) and the relative importance of abiotic parameters. (4) Finally, to

assess further the plastic response of S. americanus to different environmental conditions, reciprocal transplants could be conducted between "extreme" transects (e.g. between Reifel Refuge and Lulu Island). If that were done, exclosures should be used.

4.2 S. americanus Growth Variation Between the Fraser Estuary and the Skagit-Stillaguamish Estuary

S. americanus stems grew with much less vigour and density on the Skagit-Stillaguamish Estuary compared to those on the Fraser Estuary. That could have been due to differences in salinity (roughly 12 ppt on 11 June and 18 ppt on 24 July on the Skagit-Stillaguamish Estuary compared to 7 ppt and 13 ppt on the Fraser Estuary during similar dates), differences in Snow Goose grazing pressure (the number of Snow Goose-days experienced by the Skagit-Stillaguamish Estuary during the winter of 1986/87 was about 2.5 times that of the Fraser Estuary) or some combination of those and other factors. To better understand the growth differences between the two estuaries and the reasons for those differences, additional transects with exclosures could be established and S. americanus growth monitored over several years.

4.3 Relationships Between S. americanus Growth Indices and Biomass

The regression equations developed to predict aboveground biomass produced good results. Stem density and mean stem length accounted for most (>90%) of the variance in live and total stem biomass over the entire estuary and by transect. Stem density was the only variable able to predict belowground biomass but the amount of variance explained was lower than above, especially for root and total belowground biomass. For live rhizome biomass, the most important food source for Snow Geese, stem density explained most of its variance over the entire estuary and by transect (>73%). Although the regression lines by transect were not different, given the between-transect variation already noted for many indices, it is probably prudent to further develop separate equations for each transect.

Timing for destructive sampling was pre-determined to coincide with peak stem length, as already noted. However, peak stem density might prove to be a much better point on the growth curve at which to determine the relationships between plant growth indices and biomass, particularly for rhizome biomass. In this study, stem density was the most important and most consistent variable in the regression equations despite the fact that it must have been subject to considerable error during the time of destructive sampling (survey 7). A large proportion of stems had already been lost from the system by that time. Very few stem mortalities, however, had been observed up to and including peak density. Theoretically, stem density variance should have been smaller at that point and the amount of live rhizome biomass explained by that variable should have been greater than that calculated in this study. Therefore, another destructive sampling is recommended at peak stem density.

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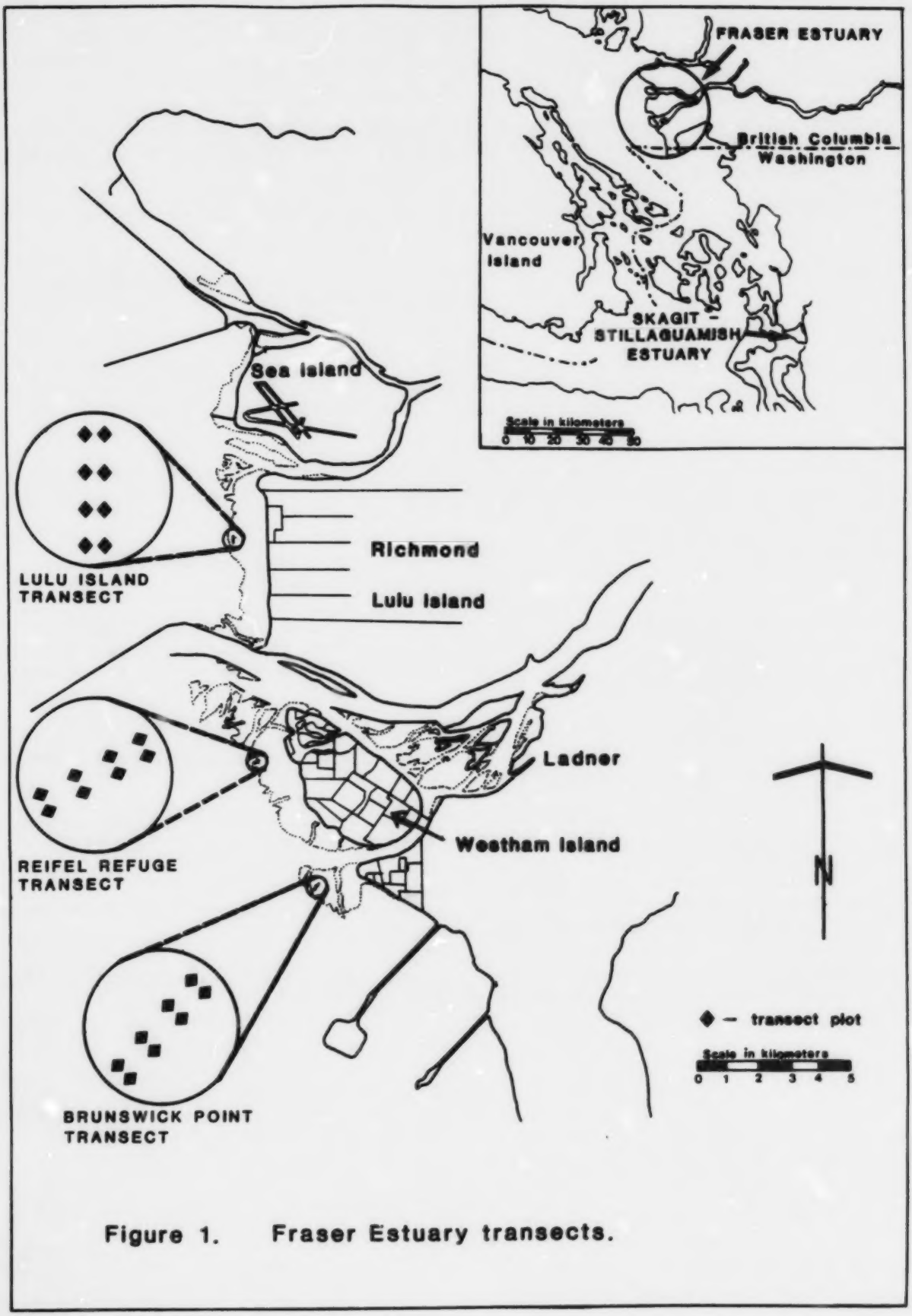

Figure 1. Fraser Estuary transects.

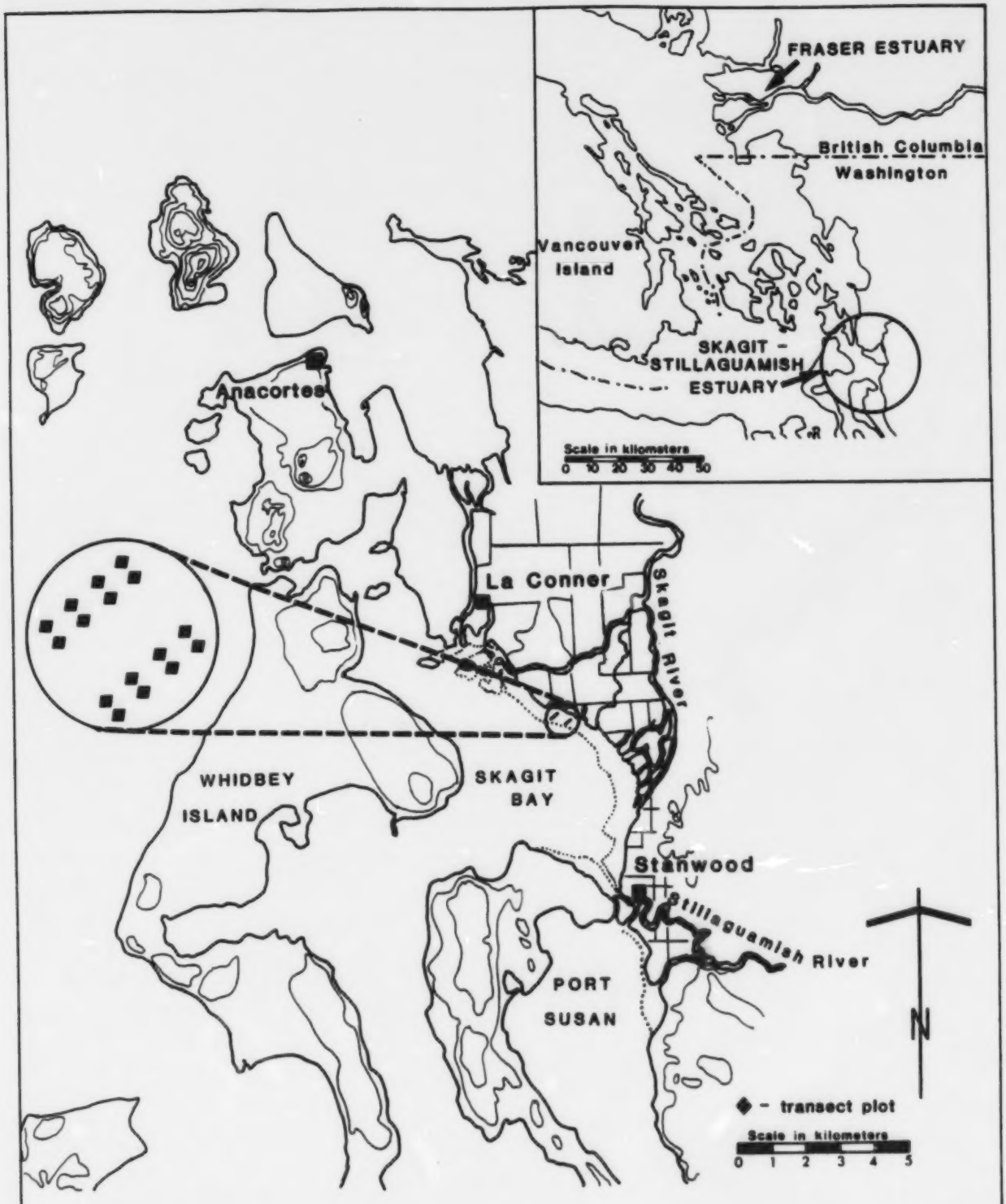

Figure 2. Skagit - Stillaguamish Estuary transects.

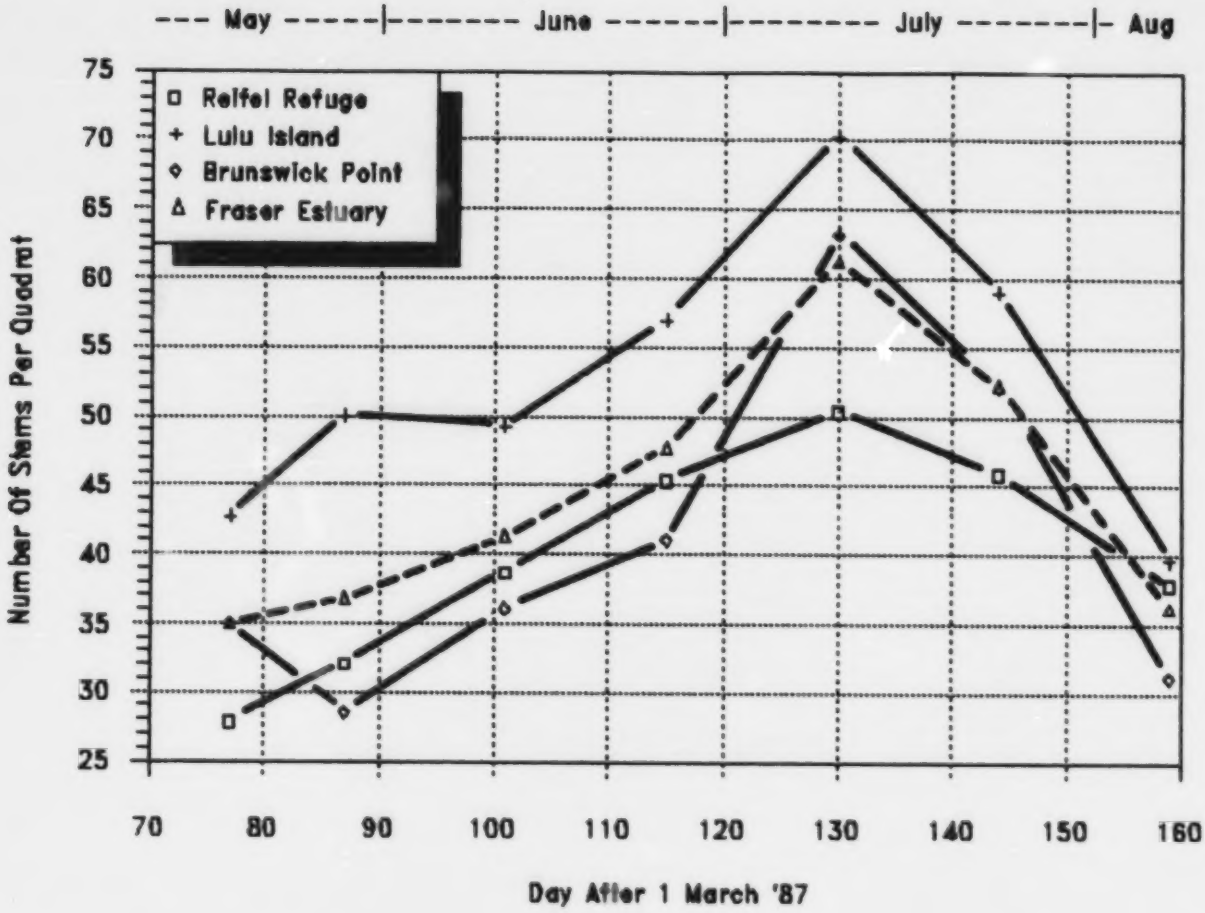

Figure 3. Stem density (live stems only) of Scirpus americanus on the Fraser Estuary 1987.

SURVEY 1

LENGTH (cm)	%	FREQ	0 10 20 30 40 50
0-10	72.5	58	+XXXX

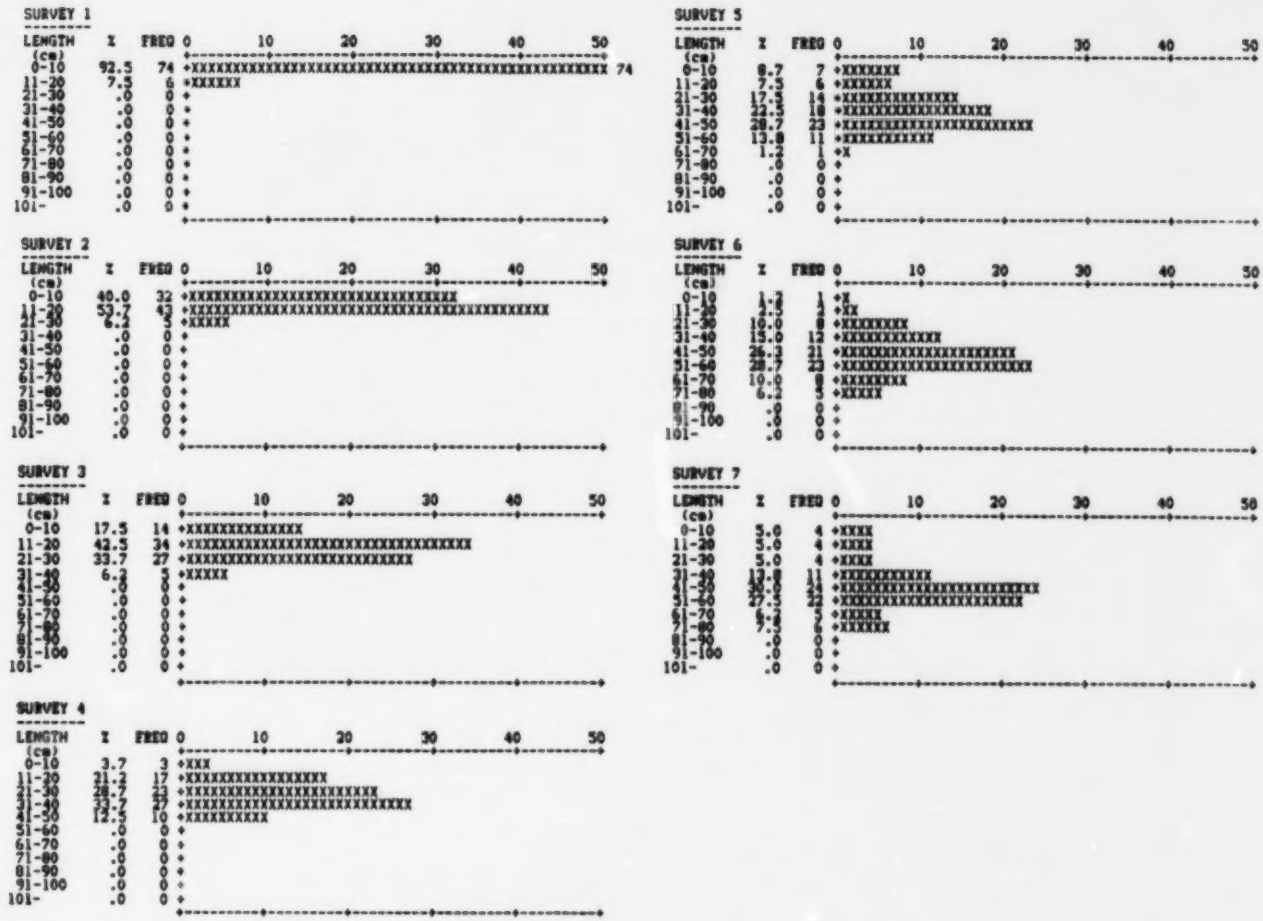

Figure 5. Frequency histograms of (total) stem length of Scirpus americanus measured in the nine non-random quadrats, Lulu Island transect 1987.

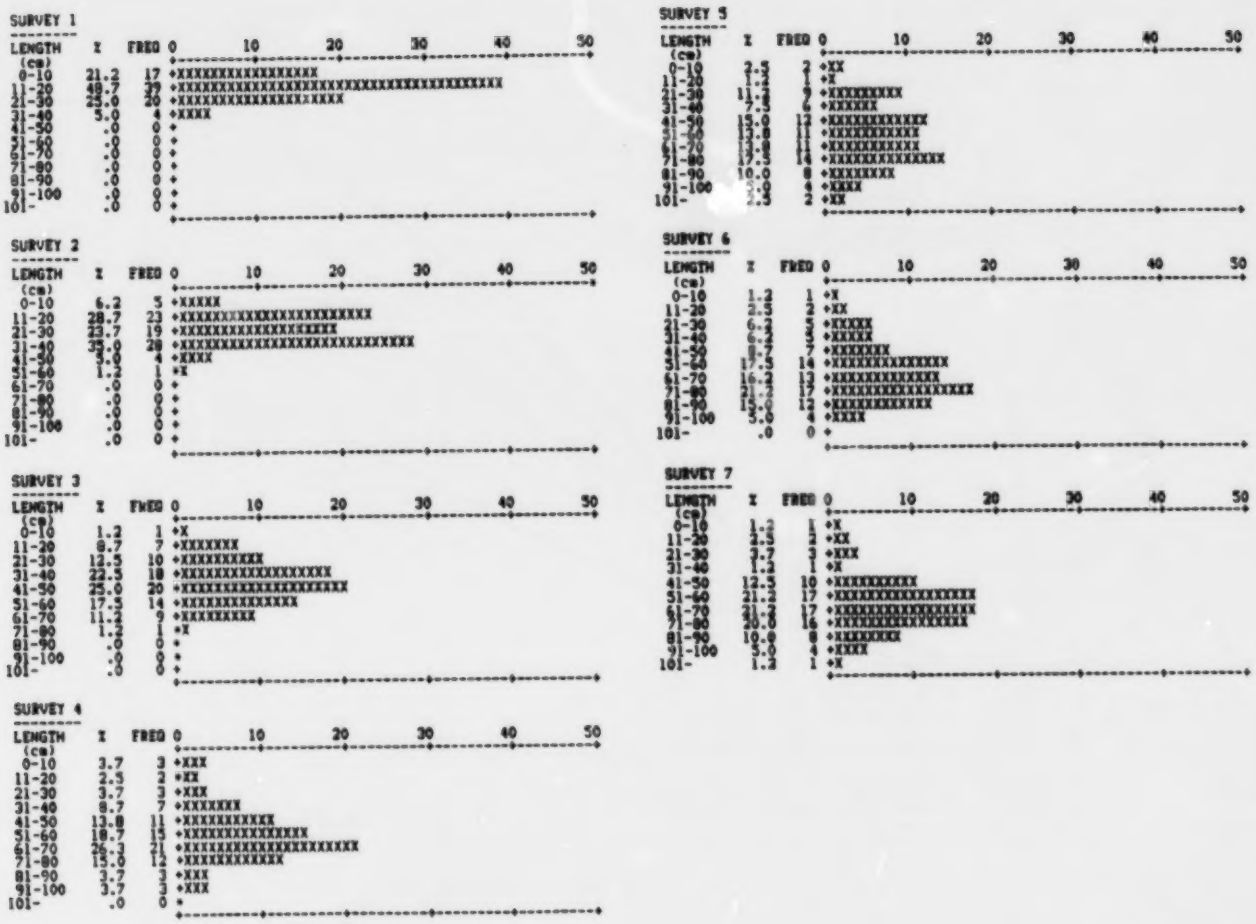
SURVEY 1
LENGTH (cm) | % | FREQ | 0 10 20 30 40 50
0-10 | 21.2 | 17 | +XXXXXXXXXXXXXXXXX
11-20 | 48.7 | 39 | +XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
21-30 | 25.0 | 20 | +XXXXXXXXXXXXXXXXXXXX
31-40 | 5.0 | 4 | +XXXX
41-50 | .0 | 0 | +
51-60 | .0 | 0 | +
61-70 | .0 | 0 | +
71-80 | .0 | 0 | +
81-90 | .0 | 0 | +
91-100 | .0 | 0 | +
101- | .0 | 0 | +
SURVEY 2
LENGTH (cm) | % | FREQ | 0 10 20 30 40 50
0-10 | 6.2 | 5 | +XXXXX
11-20 | 28.7 | 23 | +XXXXXXXXXXXXXXXXXXXXXX
21-30 | 23.7 | 19 | +XXXXXXXXXXXXXXXXXXX
31-40 | 35.0 | 28 | +XXXXXXXXXXXXXXXXXXXXXXXXXXXX
41-50 | 5.0 | 4 | +XXXX
51-60 | 1.2 | 1 | +X
61-70 | .0 | 0 | +
71-80 | .0 | 0 | +
81-90 | .0 | 0 | +
91-100 | .0 | 0 | +
101- | .0 | 0 | +
SURVEY 3
LENGTH (cm) | % | FREQ | 0 10 20 30 40 50
0-10 | 1.2 | 1 | +X
11-20 | 8.7 | 7 | +XXXXXXX
21-30 | 12.5 | 10 | +XXXXXXXXXX
31-40 | 22.5 | 18 | +XXXXXXXXXXXXXXXXXX
41-50 | 25.0 | 20 | +XXXXXXXXXXXXXXXXXXXX
51-60 | 17.5 | 14 | +XXXXXXXXXXXXXX
61-70 | 11.2 | 9 | +XXXXXXXXX
71-80 | 1.2 | 1 | +X
81-90 | .0 | 0 | +
91-100 | .0 | 0 | +
101- | .0 | 0 | +
SURVEY 4
LENGTH (cm) | % | FREQ | 0 10 20 30 40 50
0-10 | 3.7 | 3 | +XXX
11-20 | 2.5 | 2 | +XX
21-30 | 3.7 | 3 | +XXX
31-40 | 8.7 | 7 | +XXXXXXX
41-50 | 13.8 | 11 | +XXXXXXXXXXX
51-60 | 18.7 | 15 | +XXXXXXXXXXXXXXX
61-70 | 26.3 | 21 | +XXXXXXXXXXXXXXXXXXXXX
71-80 | 15.0 | 12 | +XXXXXXXXXXXX
81-90 | 3.7 | 3 | +XXX
91-100 | 3.7 | 3 | +XXX
101- | .0 | 0 | +
SURVEY 5
LENGTH (cm) | % | FREQ | 0 10 20 30 40 50
0-10 | 2.5 | 2 | +XX
11-20 | 1.2 | 1 | +X
21-30 | 11.2 | 9 | +XXXXXXXXX
31-40 | 7.5 | 6 | +XXXXXX
41-50 | 15.0 | 12 | +XXXXXXXXXXXX
51-60 | 13.8 | 11 | +XXXXXXXXXXX
61-70 | 13.8 | 11 | +XXXXXXXXXXX
71-80 | 17.5 | 14 | +XXXXXXXXXXXXX
81-90 | 10.0 | 8 | +XXXXXXXX
91-100 | 5.0 | 4 | +XXXX
101- | 2.5 | 2 | +XX
SURVEY 6
LENGTH (cm) | % | FREQ | 0 10 20 30 40 50
0-10 | 1.2 | 1 | +X
11-20 | 2.5 | 2 | +XX
21-30 | 6.2 | 5 | +XXXXX
31-40 | 6.2 | 5 | +XXXXX
41-50 | 8.7 | 7 | +XXXXXXX
51-60 | 17.5 | 14 | +XXXXXXXXXXXXX
61-70 | 16.2 | 13 | +XXXXXXXXXXXX
71-80 | 21.2 | 17 | +XXXXXXXXXXXXXXXX
81-90 | 15.0 | 12 | +XXXXXXXXXXX
91-100 | 5.0 | 4 | +XXXX
101- | .0 | 0 | +
SURVEY 7
LENGTH (cm) | % | FREQ | 0 10 20 30 40 50
0-10 | 1.2 | 1 | +X
11-20 | 2.5 | 2 | +XX
21-30 | 3.7 | 3 | +XXX
31-40 | 1.2 | 1 | +X
41-50 | 12.5 | 10 | +XXXXXXXXXX
51-60 | 21.2 | 17 | +XXXXXXXXXXXXXXXXX
61-70 | 21.2 | 17 | +XXXXXXXXXXXXXXXXX
71-80 | 20.0 | 16 | +XXXXXXXXXXXXXXXX
81-90 | 10.0 | 8 | +XXXXXXXX
91-100 | 5.0 | 4 | +XXXX
101- | 1.2 | 1 | +X

Figure 6. Frequency histograms of (total) stem length of Scirpus americanus measured in the nine non-random quadrats, Brunswick Point transect 1987.

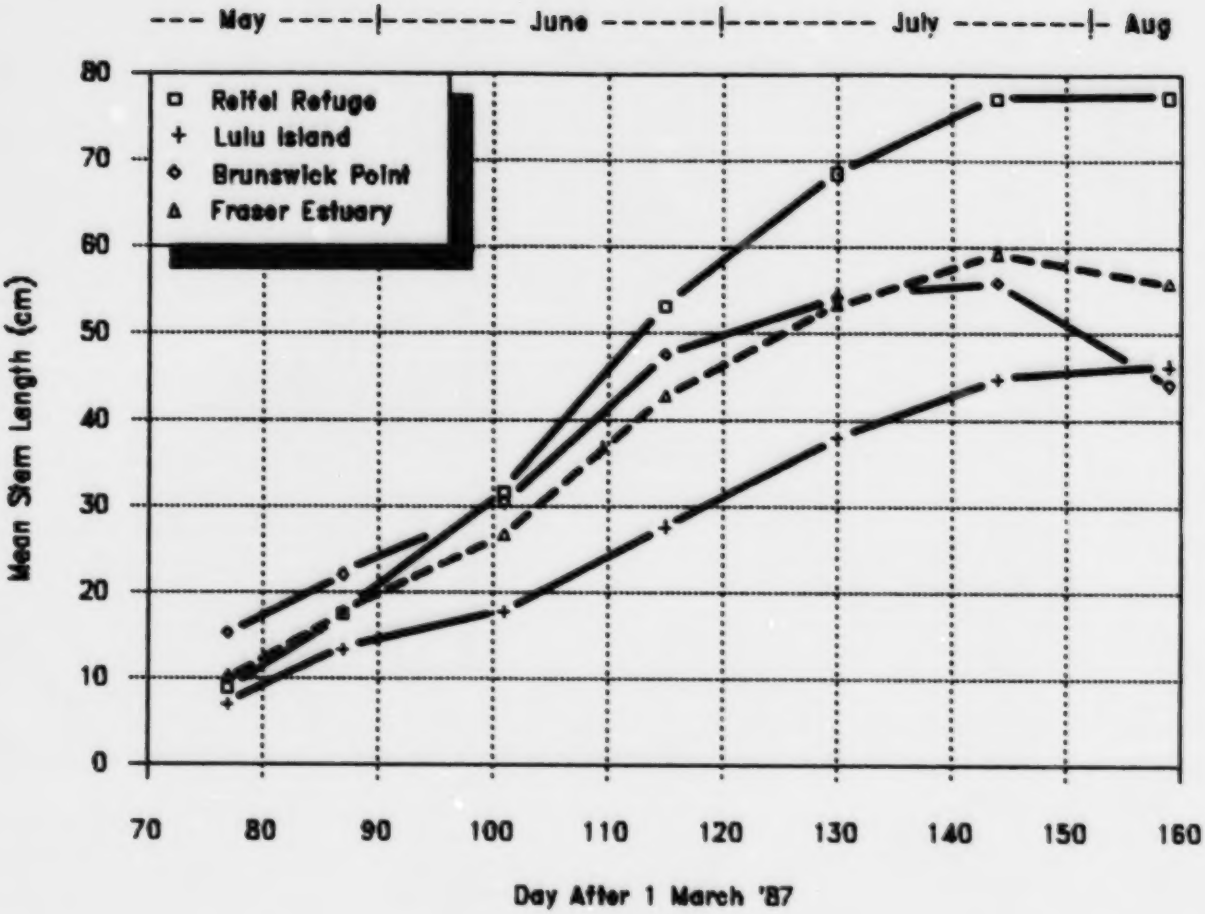

Figure 7. Mean (total) stem length of Scirpus americanus on the Fraser Estuary 1987.

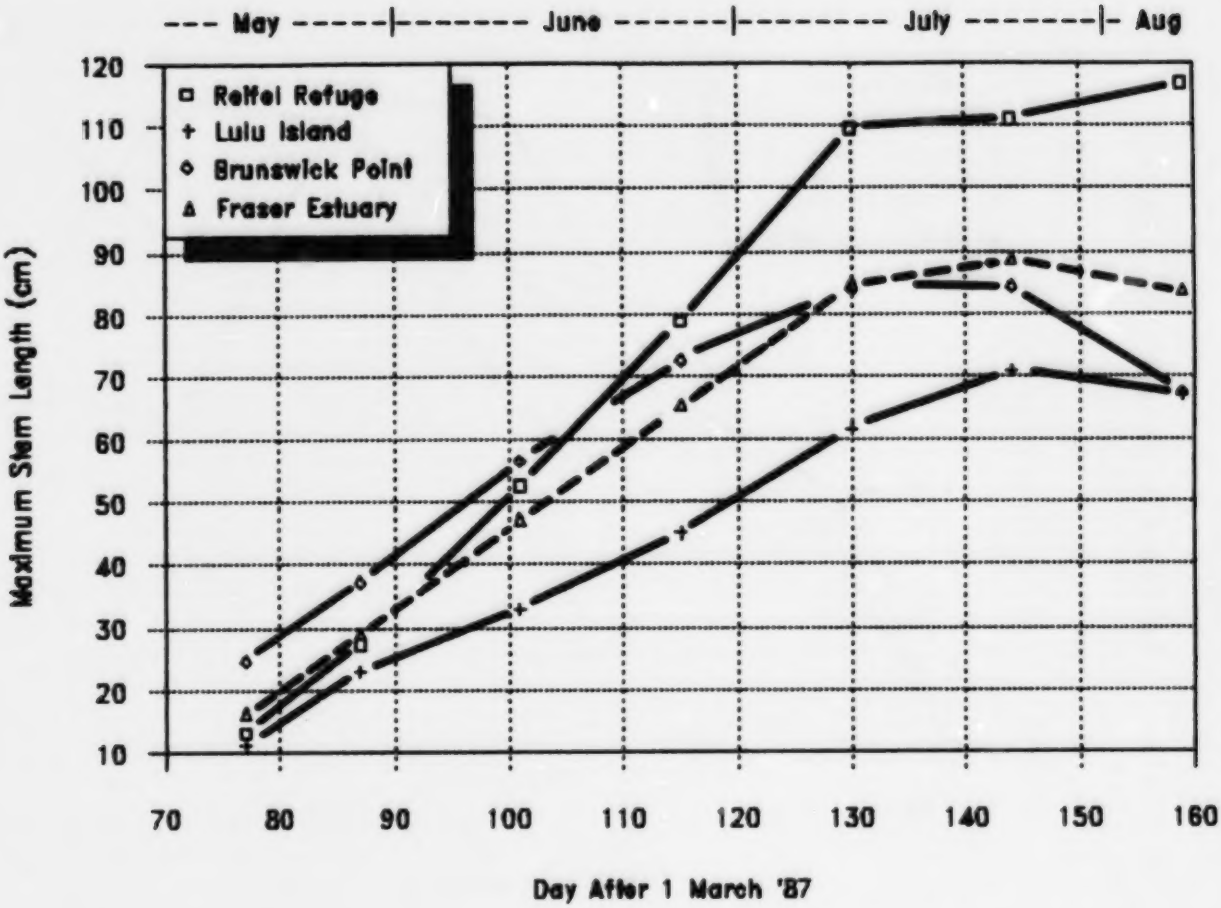

Figure 8. Maximum (total) stem length of Scirpus americanus on the Fraser Estuary 1987.

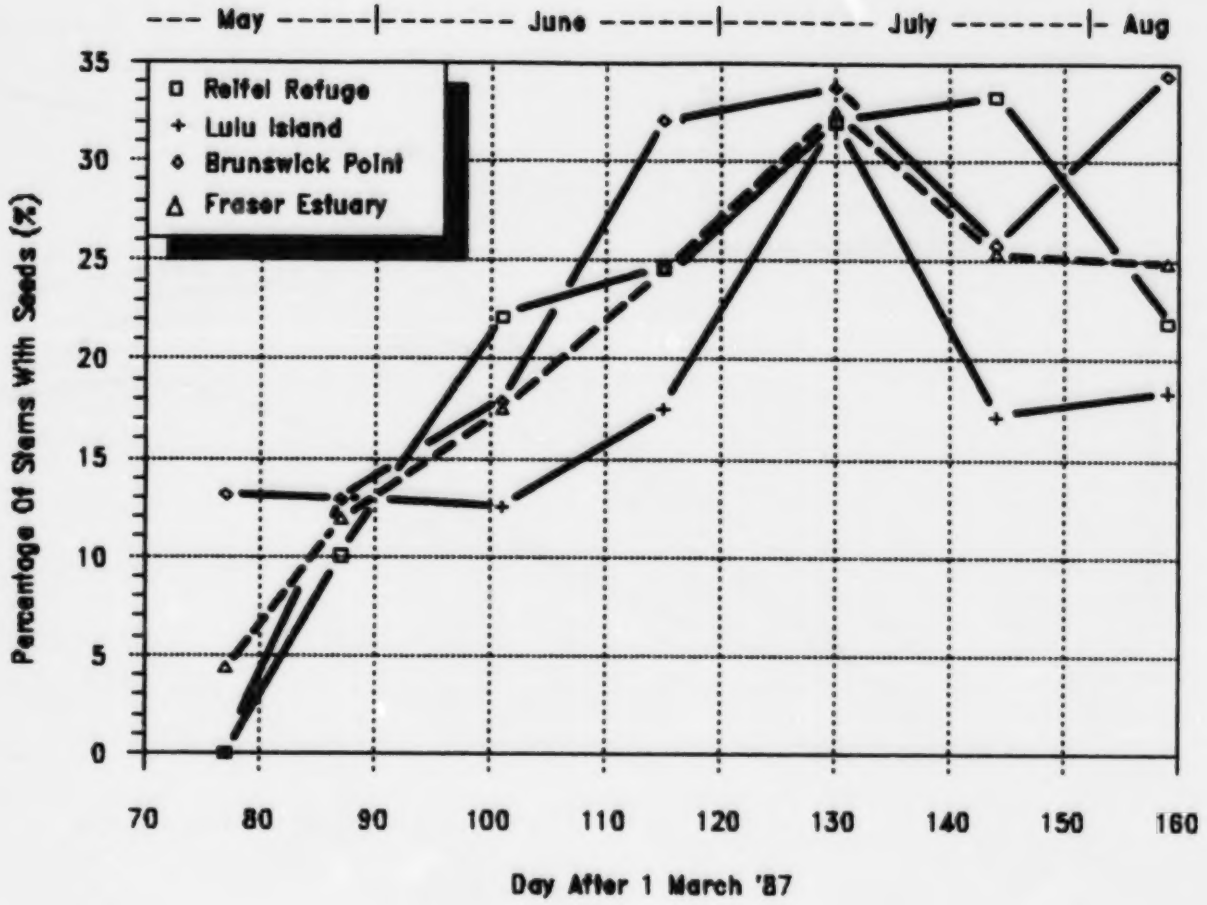

Figure 9. Relative seed abundance of Scirpus americanus on the Fraser Estuary 1987.

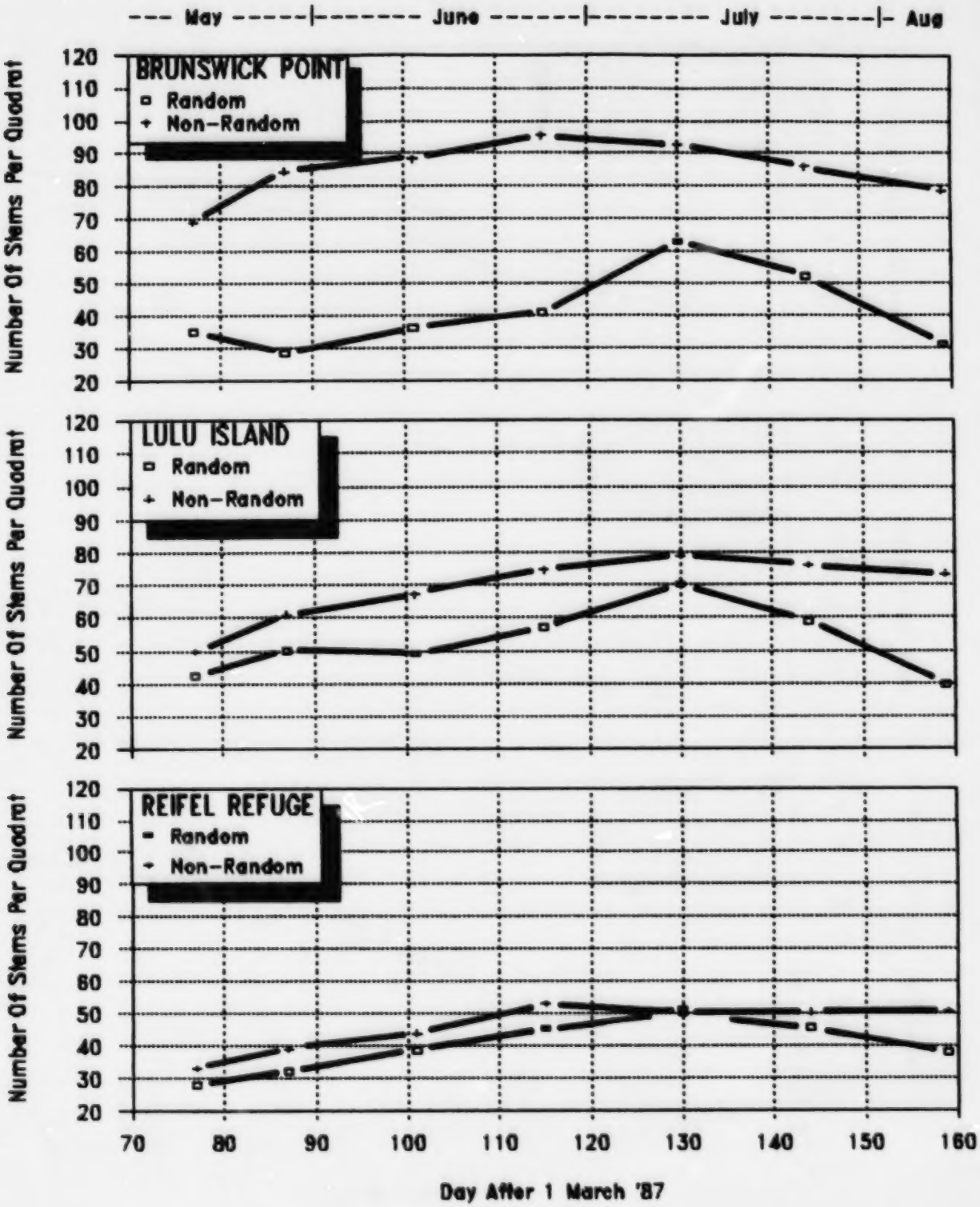

Figure 10. Stem density (live stems only) of Scirpus americanus on the Fraser Estuary 1987: random versus non-random quadrats.

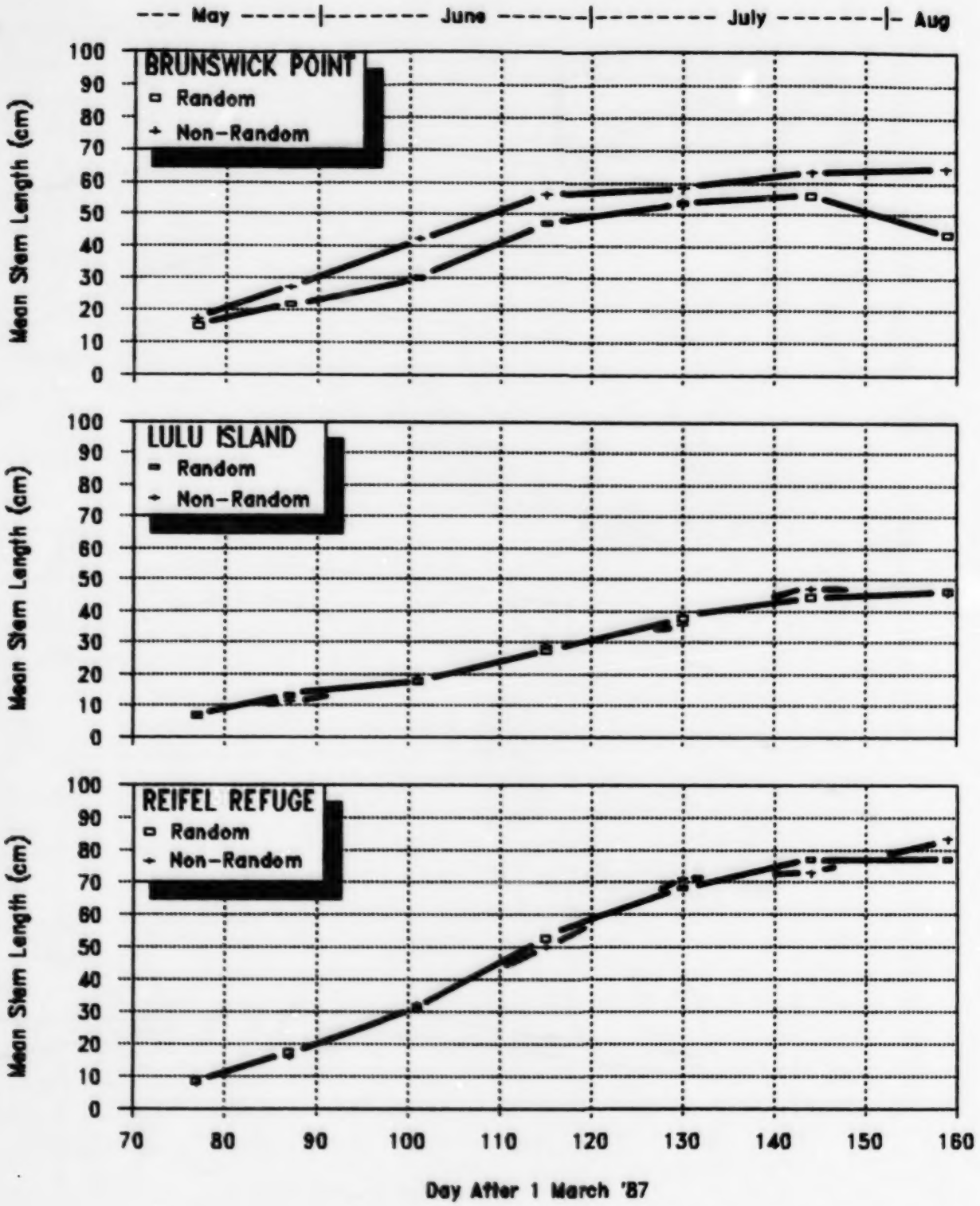

Figure 11. Mean (total) stem length of Scirpus americanus on the Fraser Estuary 1987: random versus non-random quadrats.

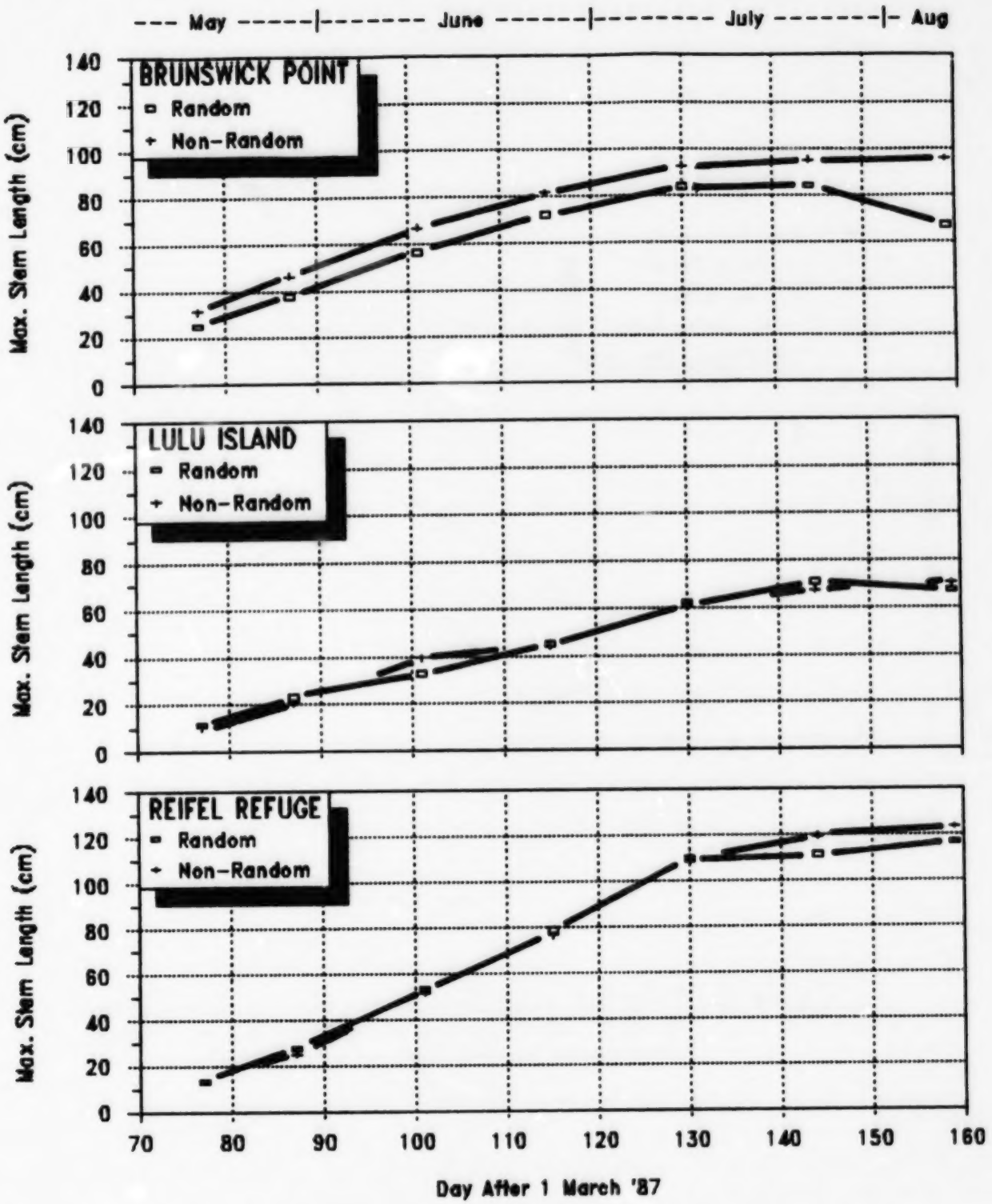

Figure 12. Maximum (total) stem length of Scirpus americanus on the Fraser Estuary 1987: random versus non-random quadrats.

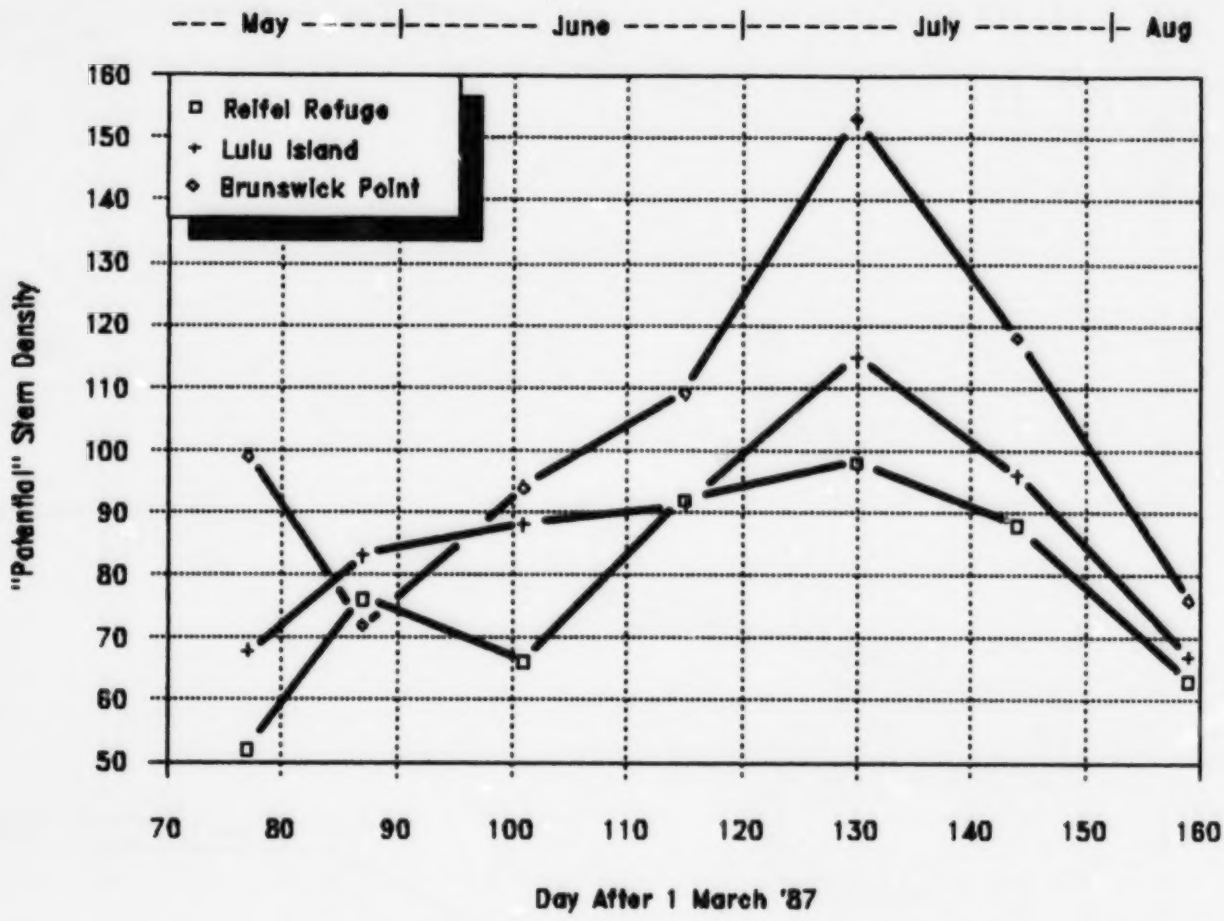

Figure 13. "Potential" stem density (number of live stems per quadrat; mean of five highest values) of Scirpus americanus on the Fraser Estuary 1987.

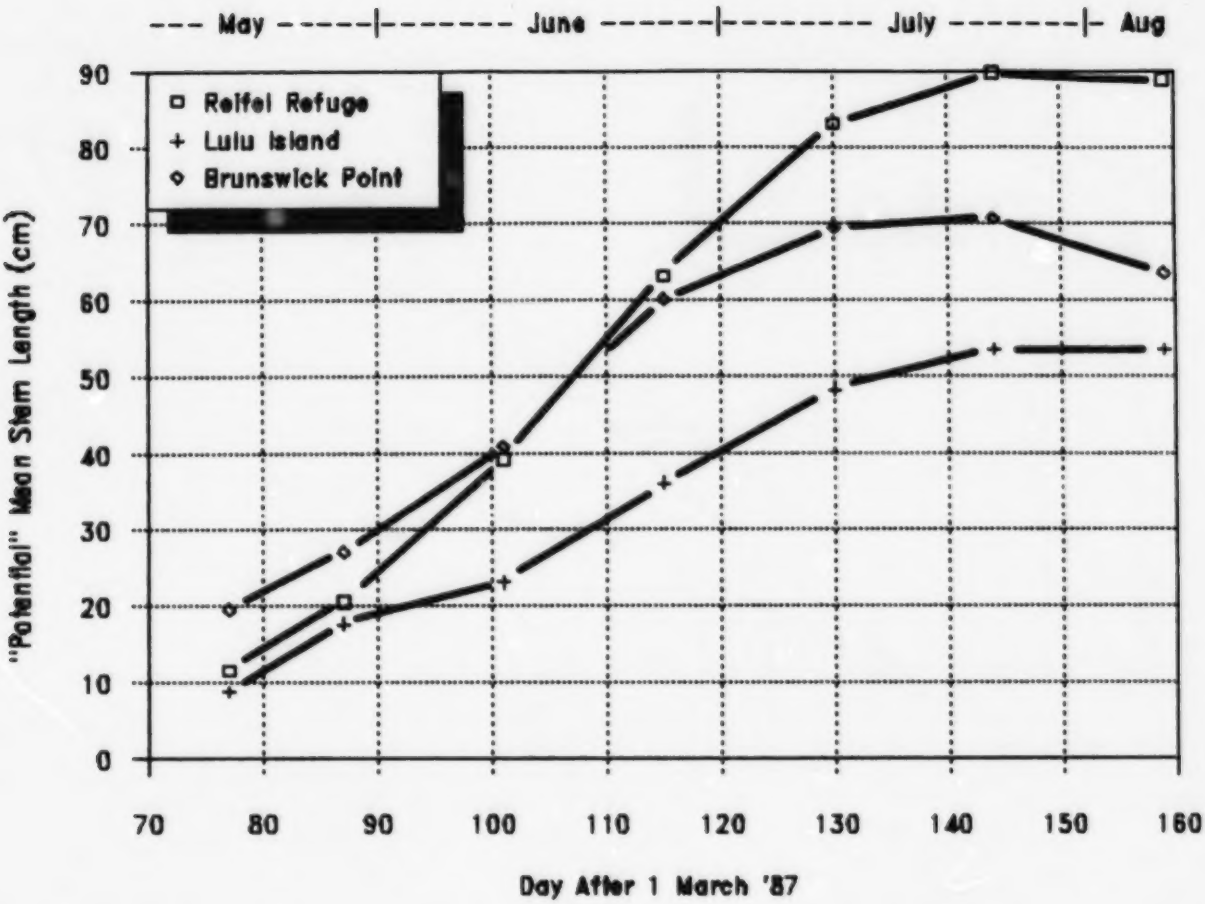

Figure 14. "Potential" mean (total) stem length (mean of five highest values) of Scirpus americanus on the Fraser Estuary 1987.

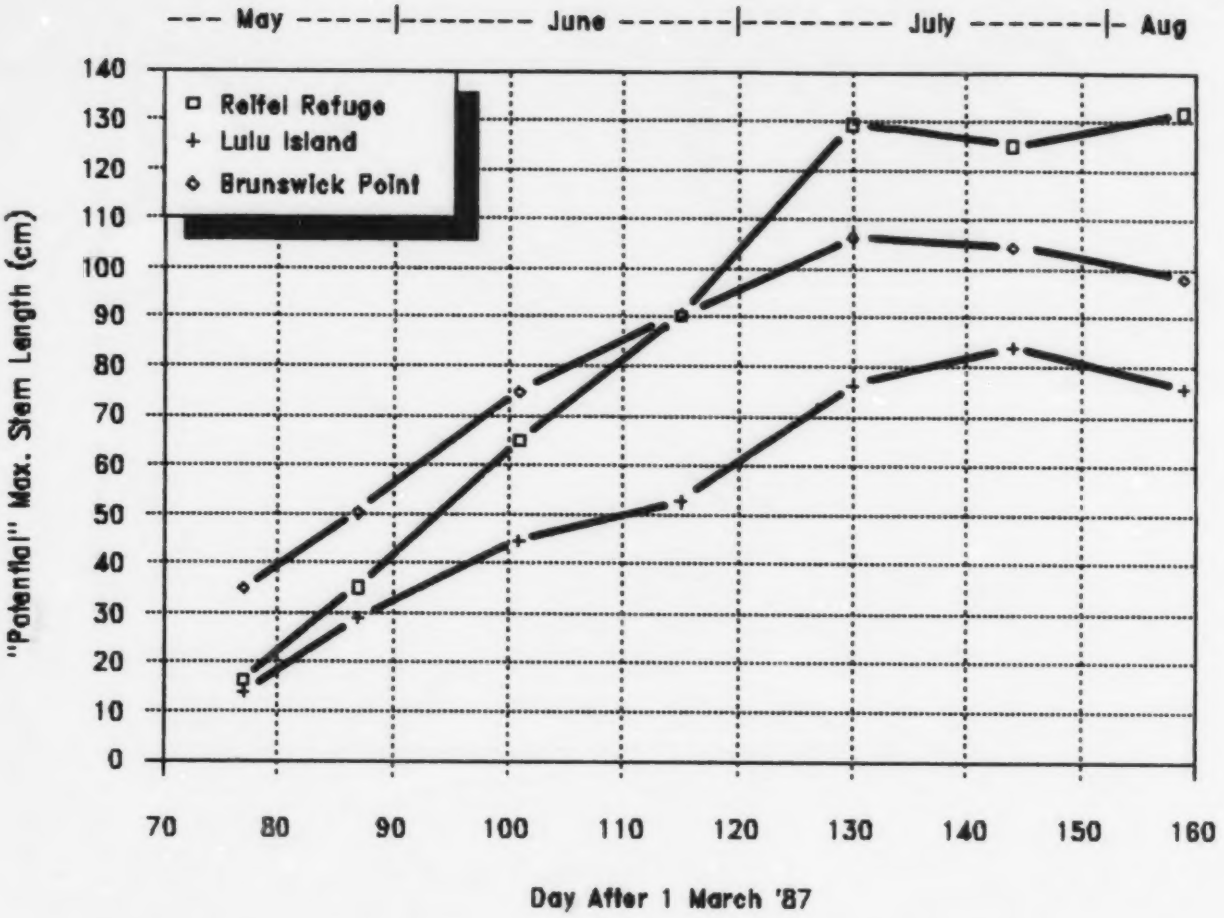

Figure 15. "Potential" maximum (total) stem length (mean of five highest values) of Scirpus americanus on the Fraser Estuary 1987.

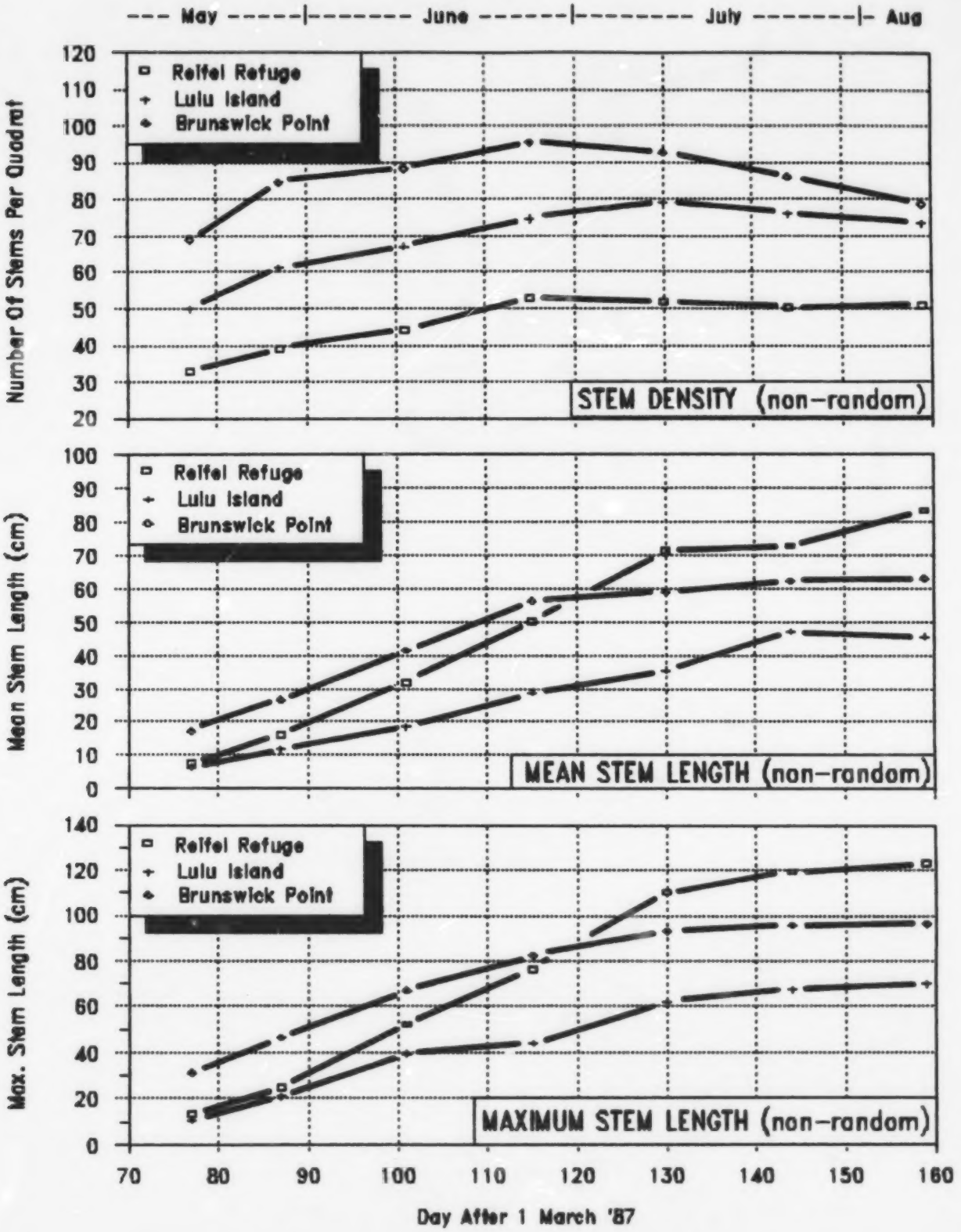

Figure 16. Scirpus americanus indices measured on the Fraser Estuary 1987: non-random quadrats only.

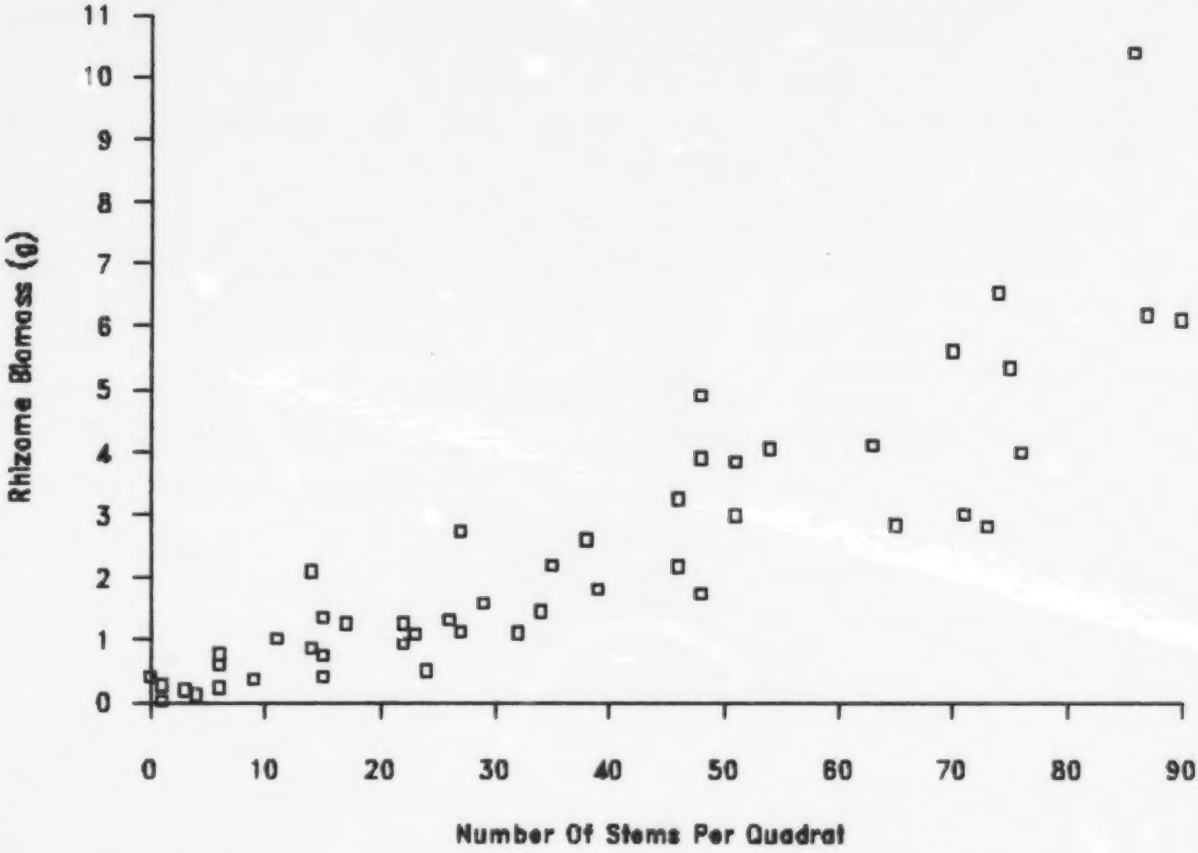

Figure 17. Scatterplot showing the relationship between Scirpus americanus rhizome biomass per core and stem density (live stems only) on the Fraser Estuary 1987.

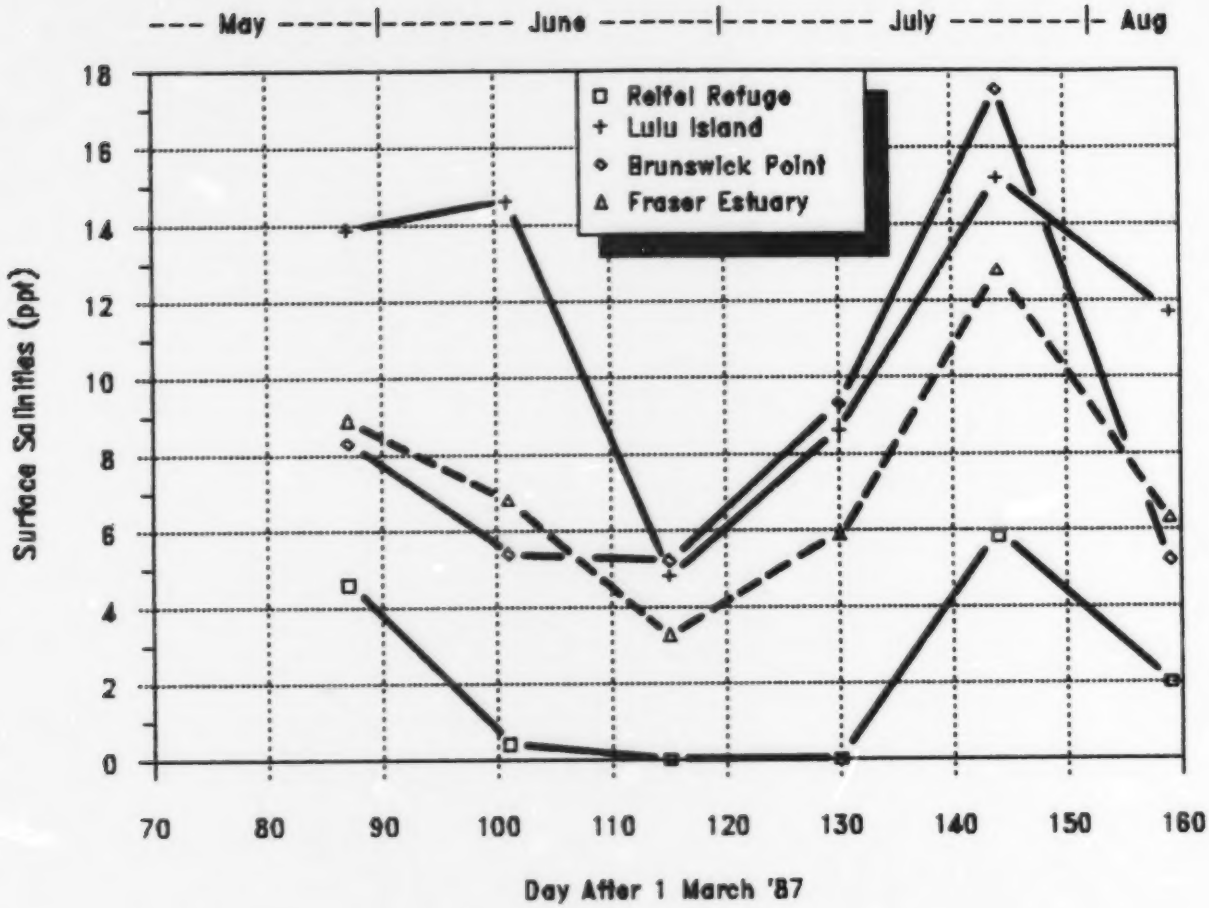

Figure 18. Surface water salinities across the Fraser Estuary 1987.

Table 1. Scirpus americanus stem density (no. stems quadrat^{-1}; live stems only; $\bar{x}\pm SE$) by transect, Fraser Estuary 1987.

Survey	1	2	3	4	5	6	7
Period (m/d)	05/13-05/19	05/25-05/27	06/08-06/10	06/22-06/24	07/07-07/09	07/21-07/23	08/05-08/07
Sample Size	16	24	24	24	24	24	16
Reifel Refuge	27.8 ± 5.0^{a}	32.0 ± 5.9^{a}	38.6 ± 4.1^{a}	$45.3\pm6.7^{a,b}$	50.4 ± 6.8^{a}	45.8 ± 5.7^{a}	37.9 ± 5.3^{a}
Lulu Island	42.7 ± 6.0^{a}	50.0 ± 5.5^{b}	49.3 ± 6.0^{a}	56.9 ± 5.2^{a}	70.2 ± 7.0^{a}	59.0 ± 5.7^{a}	39.6 ± 5.9^{a}
Brunswick Point	35.0 ± 13.4^{a}	28.5 ± 5.9^{a}	36.1 ± 7.8^{a}	41.0 ± 8.2^{b}	63.1 ± 11.4^{a}	52.0 ± 8.6^{a}	31.1 ± 8.4^{a}
Fraser Estuary (pooled data)	35.0 ± 5.1	36.8 ± 3.5	41.3 ± 3.6	47.7 ± 4.0	61.2 ± 5.0	52.3 ± 3.9	36.2 ± 3.8
Kruskal-Wallis H stat.	4.98	10.12	5.66	6.99	3.94	3.24	2.41
Prob.	>0.050	<0.010	>0.050	<0.050	>0.100	>0.100	>0.250

Notes:

1. Data were normally distributed for each survey (Kolmogorov-Smirnov goodness of fit test) but variances were unequal across transects for several surveys (Bartlett's test for homogeneity of variance). Hence, a non-parametric test (Kruskall-Wallis) was required in the analysis.

2. Letters (superscripts) denote significant similarities or differences between transects at the 5% level (that is, transects with the same letter were not statistically different whereas transects with different letters were); non-parametric multiple range test (Zar 1984).

3. Data for survey 7 resulted from the destructive sampling technique.

Table 2. *Scirpus americanus* growth indices ($\bar{x}\pm SE$), Skagit-Stillaguamish Estuary 1987.

Survey	3		6	
Date (m/d)	06/11		07/24	
	Transect A (n=48)	Transect B (n=32)	Transect A (n=32)	Transect B (n=32)
Stem Density (no. stems quadrat^{-1})	2.7±0.8	17.7±3.4	1.7±0.5	21.9±3.5
Mean Stem Length (cm)	17.1±0.6	25.4±1.1	31.3±1.3	44.9±1.4
Maximum Stem Length (cm)	27.8±1.2	42.7±1.7	43.7±1.9	61.3±2.6
Seed Abundance (percentage stems with seeds)	1.0±0.8	8.8±2.6	1.6±0.9	9.4±2.9
Stem Mortalities (as no. dead stems quadrat^{-1} and as percentage of stems present (in brackets))	0.0±0.0 (0.0)	0.0±0.0 (0.0)	0.2±0.1 (11.8)	0.4±0.2 (1.8)

Table 3. *Scirpus americanus* mean stem length (cm; live stems only; $\bar{x}\pm SE$) by transect, Fraser Estuary 1987.

Survey Period (m/d) Sample Size	1 05/13-05/19 16	2 05/25-05/27 24	3 06/08-06/10 24	4 06/22-06/24 24	5 07/07-07/09 24	6 07/21-07/23 24	7 08/05-08/07 16
Reifel Refuge	8.7±0.6[a]	17.3±0.5[a]	31.5±1.1[a]	52.9±1.7[a]	68.3±2.5[a]	77.1±1.8[a]	77.2±2.6[a]
Lulu Island	6.8±0.5[a]	13.2±0.6[b]	17.7±0.8[b]	27.5±1.5[b]	37.8±1.5[b]	44.6±1.6[b]	46.1±1.6[b]
Brunswick Point	15.2±0.9[b]	21.9±0.8[c]	30.3±1.5[a]	47.3±2.1[a]	53.9±2.4[c]	55.7±2.2[c]	43.9±4.9[b]
Fraser Estuary (pooled data)	10.2±0.7	17.5±0.6	26.5±1.0	42.6±1.6	53.3±1.9	59.1±1.9	55.7±2.9
Kruskal-Wallis H stat.	30.94	43.15	43.76	44.26	43.73	42.26	28.96
Prob.	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

Note: See notes at the bottom of Table 1.

Table 4. Scirpus americanus maximum stem length (cm; live stems only; $\bar{x}\pm SE$) by transect, Fraser Estuary 1987.

Survey Period (m/d) Sample Size	1 05/13-05/19 16	2 05/25-05/27 24	3 06/08-06/10 24	4 06/22-06/24 24	5 07/07-07/09 24	6 07/21-07/23 24	7 08/05-08/07 16
Reifel Refuge	13.1±0.7[a]	27.3±1.2[a]	52.6±1.7[a]	78.8±1.6[a]	109.4±2.7[a]	111.1±3.6[a]	116.7±3.4[a]
Lulu Island	11.3±0.6[a]	22.9±0.9[a]	32.9±2.2[b]	45.0±1.4[b]	61.6±2.7[b]	70.8±2.1[b]	67.0±1.8[b]
Brunswick Point	24.6±2.1[b]	37.3±2.3[b]	56.5±2.7[a]	72.4±3.5[a]	83.8±5.0[c]	84.3±3.2[c]	67.3±7.3[b]
Fraser Estuary (pooled data)	16.3±1.1	29.1±1.1	47.3±1.8	65.4±2.2	84.9±3.1	88.7±2.6	83.7±4.3
Kruskal-Wallis H stat.	27.05	26.64	38.94	39.52	45.86	41.93	29.81
Prob.	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

Note: See notes at the bottom of Table 1.

Table 5. Scirpus americanus percentage of stems containing seedheads (%; live stems only; $\bar{x}$+SE) by transect, Fraser Estuary 1987.

Survey Period (m/d) Sample Size	1 05/13-05/19 16	2 05/25-05/27 24	3 06/08-06/10 24	4 06/22-06/24 24	5 07/07-07/09 24	6 07/21-07/23 24	7 08/05-08/07 16
Reifel Refuge	0.0±0.0[a]	10.0±3.0[a]	22.1±5.4[a]	24.6±5.0[a]	32.1±5.4[a]	33.3±5.3[a]	21.9±4.2[a]
Lulu Island	0.0±0.0[a]	12.9±4.1[a]	12.5±4.0[a]	17.5±4.7[a]	31.7±4.0[a]	17.1±4.3[b]	18.4±3.2[a]
Brunswick Point	13.1±3.9[b]	12.9±3.6[a]	17.9±4.3[a]	32.1±5.4[a]	33.8±6.5[a]	25.8±4.0[a,b]	34.4±6.8[a]
Fraser Estuary (pooled data)	4.4±1.6	11.9±2.1	17.5±2.7	24.7±3.0	32.5±3.1	25.4±2.7	24.9±3.0
Kruskall Wallis H stat.	21.40	0.32	1.58	4.76	0.03	6.70	2.81
Prob.	<0.001	>0.750	>0.250	>0.050	>0.975	<0.050	>0.100

Notes:

1. See notes at the bottom of Table 1.

2. Quadrats for surveys 1 through 6 were random; those for survey 7 were non-random. The number of stems containing seedheads were not recorded in the destructive technique.

Table 6. *Scirpus americanus* stem mortalities (no. dead stems quadrat^{-1} and percentage of live plus dead stems; $\bar{x}\pm SE$) by transect during surveys 6 and 7, Fraser Estuary 1987. (n=32 per transect for survey 6 and n=16 for survey 7; n=96 for the entire estuary for survey 6 and n=48 for survey 7.)

Survey Period (m/d)	6 07/21-07/23		7 08/05-08/07	
	Number Quadrat^{-1}	%	Number Quadrat^{-1}	%
Reifel Refuge	0.7 ± 0.2^a	1.4	1.7 ± 0.3^a	3.2
Lulu Island	3.3 ± 0.3^b	4.7	5.4 ± 0.8^b	6.9
Brunswick Point	4.3 ± 0.5^b	5.9	5.7 ± 1.0^b	6.8
Fraser Estuary (pooled data)	2.7 ± 0.3	4.0	4.3 ± 0.5	5.6
Kruskal-Wallis H stat.	27.44		20.31	
Prob.	<0.001		<0.001	

Notes:

1. See notes at the bottom of Table 1.

2. Stem mortalities (i.e. stems completely senesced, with total loss of green colour) were not recorded during surveys 1 through 5. Dead stems were observed, however, by survey 5 and they were likely present in small numbers during earlier surveys.

3. For survey 6, data from two random plus two non-random quadrats per plot were used whereas for survey 7, data from only two non-random quadrats per plot were used. The number of dead stems were not recorded in the destructive technique.

Table 7. Scirpus americanus aboveground growth indices (live stems only; $\bar{x}\pm SE$) by transect during survey 7, Fraser Estuary 1987. (n=16 per transect; n=48 for the entire estuary).

Index	Reifel Refuge	Lulu Island	Brunswick Point	Fraser Estuary (pooled data)	Kruskall-Wallis H. stat.	Prob.
Stem Density (no. stems quadrat^{-1})	37.9±5.3^{a}	39.6±5.9^{a}	31.1±8.5^{a}	36.2±3.8	2.41	>0.250
Mean Stem Length (live portion)(cm)	54.1±2.2^{a}	30.4±1.7^{b}	30.5±4.1^{b}	38.4±2.3	23.57	<0.001
Mean Stem Length (total) (cm)	77.2±2.6^{a}	46.1±1.6^{b}	43.9±4.9^{b}	55.7±2.9	28.96	<0.001
Maximum Stem Length (live portion) (cm)	103.1±4.2^{a}	50.7±2.3^{b}	52.3±6.7^{b}	68.7±4.4	28.12	<0.001
Maximum Stem Length (total) (cm)	116.7±3.4^{a}	67.0±1.8^{b}	67.3±7.3^{b}	83.7±4.3	29.81	<0.001
Mean Stem Basal Diameter (mm)	4.2±0.1^{a}	3.1±0.1^{b}	3.1±0.3^{b}	3.5±0.1	20.03	<0.001
Live Stem Biomass (live stems only) (g quadrat^{-1})	15.098±2.319^{a}	7.533±1.119^{a,b}	8.062±2.585^{b}	10.231±1.292	7.88	<0.025
Total Stem Biomass (live plus dead stems) (g quadrat^{-1})	16.108±2.512^{a}	7.932±1.128^{a,b}	9.294±2.912^{b}	11.112±1.407	7.45	<0.025
Mean Biomass per Stem (live stems only)(g)	0.409±0.022^{a}	0.203±0.015^{b}	0.194±0.026^{b}	0.269±0.019	26.66	<0.001
Mean Biomass per Stem (live plus dead stems)(g)	0.435±0.023^{a}	0.219±0.015^{b}	0.225±0.029^{b}	0.293±0.020	25.38	<0.001

Note: See notes at the bottom of Table 1.

Table 8. *Scirpus americanus* belowground indices (g core^{-1}; $\bar{x}\pm SE$) for top and bottom core subsamples during survey 7, Fraser Estuary 1987. (n=96 for all indices).

Index	Subsample		Paired-sample T test	
	Top 15cm	Bottom 15cm	T value	Prob.
1. Live Rhizome Biomass	1.273±0.112	1.105±0.133	1.93	0.057
2. Total Rhizome Biomass (live plus dead)	1.323±0.114	1.172±0.133	1.67	0.098
3. Root Biomass	4.609±0.313	3.281±0.261	4.61	<0.001
4. Total Rhizome plus Root Biomass	5.931±0.379	4.453±0.338	4.43	<0.001
5. Total Belowground Biomass	6.342±0.397	4.612±0.341	5.10	<0.001

Notes:

1. All indices were normally distributed (Kolmogorov-Smirnov goodness of fit test), permitting analysis by Paired-sample T tests. Because of their small proportions (see below), their non-importance to grazing geese, and the fact that they tended to have non-normal distributions, dead rhizomes and miscellaneous plant material were not considered separately in this analysis.

2. Dead rhizomes and miscellaneous plant material constituted only 0.7 and 6.4% of the total belowground plant biomass in the top core subsamples and only 1.5 and 3.4% of the total belowground biomass in the bottom core subsamples, respectively.

Table 9. *Scirpus americanus* belowground indices (g core^{-1}; $\bar{x}\pm SE$) for top and bottom core subsamples during survey 7, Reifel Refuge transect 1987. (n=32 for all indices).

Index	Subsample		Paired-sample T test	
	Top 15cm	Bottom 15cm	T value	Prob.
1. Live Rhizome Biomass	1.317±0.152	1.273±0.204	0.31	0.761
2. Total Rhizome Biomass (live plus dead)	1.334±0.153	1.274±0.204	0.42	0.681
3. Root Biomass	4.626±0.444	3.648±0.444	2.05	0.049
4. Total Rhizome plus Root Biomass	5.960±0.541	4.922±0.594	1.96	0.059
5. Total Belowground Biomass	6.355±0.565	5.001±0.593	2.55	0.016

Notes:

1. See note 1 at the bottom of Table 8.

2. Dead rhizomes and miscellaneous plant material constituted only 0.3 and 6.2% of the total belowground plant biomass in the top core subsamples and only 0.0 and 1.6% of the total belowground biomass in the bottom core subsamples, respectively.

Table 10. *Scirpus americanus* belowground indices (g core^{-1}; $\bar{x}\pm SE$) for top and bottom core subsamples during survey 7, Lulu Island transect 1987. (n=32 for all indices).

Index	Subsample		Paired-sample T test	
	Top 15cm	Bottom 15cm	T value	Prob.
1. Live Rhizome Biomass	1.302±0.175	0.863±0.167	3.09	0.004
2. Total Rhizome Biomass (live plus dead)	1.422±0.183	1.039±0.167	2.48	0.019
3. Root Biomass	6.475±0.571	4.289±0.466	3.47	0.002
4. Total Rhizome plus Root Biomass	7.897±0.658	5.327±0.480	3.66	0.001
5. Total Belowground Biomass	8.362±0.682	5.520±0.493	4.02	<0.001

Notes:

1. See note 1 at the bottom of Table 8.

2. Dead rhizomes and miscellaneous plant material constituted only 1.4 and 5.6% of the total belowground plant biomass in the top core subsamples and only 3.2 and 3.5% of the total belowground biomass in the bottom core subsamples, respectively.

Table 11. *Scirpus americanus* belowground indices (g core^{-1}; $\bar{x}\pm SE$) for top and bottom core subsamples during survey 7, Brunswick Point transect 1987. (n=32 for all indices).

Index	Subsample		Paired-sample T test	
	Top 15cm	Bottom 15cm	T value	Prob.
1. Live Rhizome Biomass	1.200±0.246	1.178±0.301	0.14	0.892
2. Total Rhizome Biomass (live plus dead)	1.210±0.247	1.204±0.303	0.04	0.968
3. Root Biomass	2.727±0.388	1.905±0.338	2.54	0.016
4. Total Rhizome plus Root Biomass	3.937±0.585	3.109±0.614	1.88	0.069
5. Total Belowground Biomass	4.308±0.630	3.312±0.620	2.14	0.040

Notes:

1. See note 1 at the bottom of Table 8.

2. Dead rhizomes and miscellaneous plant material constituted only 0.2 and 8.6% of the total belowground plant biomass in the top core subsamples and only 0.8 and 6.1% of the total belowground biomass in the bottom core subsamples, respectively.

Table 12. Scirpus americanus belowground indices (g core^{-1}; $\bar{x}\pm$SE) by transect during survey 7, Fraser Estuary 1987. The top and bottom core subsamples were added and the two cores per quadrat averaged. (n=16 per transect; n=48 for the entire estuary).

Index	Reifel Refuge	Lulu Island	Brunswick Point	Fraser Estuary (pooled data)	ANOVA F ratio	Prob.
1. Live Rhizome Biomass	2.589±0.454[a]	2.165±0.404[a]	2.378±0.728[a]	2.377±0.310	0.14	0.861
2. Total Rhizome Biomass (live plus dead)	2.608±0.456[a]	2.460±0.396[a]	2.414±0.730[a]	2.494±0.309	0.03	0.966
3. Root Biomass	8.274±1.009[a]	10.764±1.163[a]	4.632±0.856[b]	7.890±0.682	9.19	<0.001
4. Total Rhizome plus Root Biomass	10.882±1.385[a,b]	13.224±1.281[a]	7.046±1.534 [b]	10.384±0.876	4.93	0.011
5. Total Belowground Biomass	11.356±1.421[a,b]	13.882±1.350[a]	7.620±1.600 [b]	10.953±0.906	4.65	0.014

Notes:

1. All indices were normally distributed (Kolmogorov-Smirnov goodness of fit test) and their variances were equal across transects (Bartlett's test for homogeneity of variances), permitting analysis by One-way ANOVA. Because of their small proportions (see below), their non-importance to grazing geese, and the fact that they tended to have non-normal distributions, dead rhizomes and miscellaneous plant material were not considered separately in this analysis.

2. Dead rhizomes and miscellaneous plant material constituted only 0.2 and 4.2%, 2.1 and 4.7%, and 0.5 and 7.5% of the total belowground plant biomass at Reifel Refuge, Lulu Island, and Brunswick Point, respectively. They constituted only 1.1 and 5.2% of the total belowground plant biomass in the Fraser Estuary (pooled data).

Table 13. *Scirpus americanus* belowground indices (g core^{-1}; $\bar{x}\pm SE$) for bottom core subsamples by transect during survey 7, Fraser Estuary 1987. The two bottom core subsamples per quadrat were averaged. (n=16 per transect; n=48 for the entire estuary).

Index	Reifel Refuge	Lulu Island	Brunswick Point	Fraser Estuary (pooled data)	ANOVA F ratio	Prob.
1. Live Rhizome Biomass	1.273±0.272[a]	0.863±0.222[a]	1.178±0.423[a]	1.105±0.181	0.45	0.635
2. Total Rhizome Biomass (live plus dead)	1.274±0.272[a]	1.039±0.212[a]	1.204±0.425[a]	1.172±0.179	0.14	0.864
3. Root Biomass	3.648±0.608[a]	4.289±0.621[a]	1.905±0.456[b]	3.280±0.352	4.74	0.013
4. Total Rhizome plus Root Biomass	4.981±0.783[a,b]	5.710±0.664[a]	3.116±0.726[b]	4.602±0.440	3.39	0.042
5. Total Belowground Biomass	6.039±0.705[a,b]	8.089±0.896[a]	4.140±0.769[b]	6.089±0.506	6.18	0.004

Notes:

1. See note 1 at the bottom of Table 12.

2. Dead rhizomes and miscellaneous plant material constituted only 0.0 and 1.3%, 2.2 and 2.4%, and 0.6 and 4.9% of the total belowground plant biomass (bottom subsamples) at Reifel Refuge, Lulu Island and Brunswick Point, respectively. They constituted only 1.1 and 2.6% of the total belowground biomass (bottom subsamples) in the Fraser Estuary (pooled data).

Table 14. *Scirpus americanus* belowground indices (g core^{-1}; $\bar{x}\pm SE$) for top core subsamples by transect during survey 7, Fraser Estuary 1987. The two top core subsamples per quadrat were averaged. (n=16 per transect; n=48 for the entire estuary).

Index	Reifel Refuge	Lulu Island	Brunswick Point	Fraser Estuary (pooled data)	ANOVA F ratio	Prob.
1. Live Rhizome Biomass	1.316±0.201[a]	1.302±0.209[a]	1.200±0.328[a]	1.273±0.143	0.06	0.939
2. Total Rhizome Biomass (live plus dead)	1.334±0.204[a]	1.422±0.217[a]	1.210±0.329[a]	1.322±0.145	0.17	0.842
3. Root Biomass	4.626±0.573[a]	6.475±0.770[b]	2.726±0.479[c]	4.609±0.415	9.15	<0.001
4. Total Rhizome plus Root Biomass	5.960±0.706[a,b]	7.897±0.878[a]	3.937±0.761[b]	5.931±0.502	6.36	0.003
5. Total Belowground Biomass	6.355±0.741[a,b]	8.362±0.918[a]	4.308±0.825[b]	6.342±0.528	5.94	0.005

Notes:

1. See note 1 at the bottom of Table 12.

2. Dead rhizomes and miscellaneous plant material constituted only 0.3 and 6.2%, 1.4 and 5.6%, and 0.2 and 8.6% of the total belowground plant biomass (top subsamples) at Reifel Refuge, Lulu Island and Brunswick Point, respectively. They constituted only 0.8 and 6.5% of the total belowground biomass (top subsamples) in the Fraser Estuary (pooled data).

Table 15. *Scirpus americanus* biomass and ratio values ($\bar{x}$+SE) by transect during survey 7, Fraser Estuary 1987. (n=16 per transect; n=48 for the entire estuary).

Index	Reifel Refuge	Lulu Island	Brunswick Point	Fraser Estuary (pooled data)	Kruskall -Wallis H. stat.	Prob.
Biomass:						
Aboveground Biomass ($g\ m^{-2}$)	257 ± 40^{a}	$126\pm18^{a,b}$	148 ± 46^{b}	177 ± 22	7.457	<0.025
Belowground Biomass ($g\ m^{-2}$)	$924\pm115^{a,b}$	1129 ± 109^{a}	620 ± 130^{b}	891 ± 73	8.646	<0.025
Total Biomass ($g\ m^{-2}$)	1181 ± 148^{a}	1256 ± 116^{a}	768 ± 166^{a}	1069 ± 87	5.925	>0.050
Ratios:						
Aboveground: Belowground	0.284 ± 0.024^{a}	0.122 ± 0.017^{b}	0.195 ± 0.047^{b}	0.200 ± 0.021	14.174	<0.001
Aboveground: Rhizome	1.531 ± 0.180^{a}	0.883 ± 0.127^{b}	0.815 ± 0.205^{b}	1.077 ± 0.109	13.579	<0.005
Aboveground: Root	0.396 ± 0.040^{a}	0.171 ± 0.030^{b}	$0.365\pm0.107^{a,b}$	0.311 ± 0.041	11.520	<0.005
Root:Rhizome	4.736 ± 1.020^{a}	7.446 ± 1.213^{a}	7.207 ± 3.420^{a}	6.463 ± 1.242	5.512	>0.050

Notes:

1. All indices were normally distributed (Kolmogorov-Smirnov goodness of fit test) but total aboveground biomass and all ratios had unequal variances across transects (Bartlett's test for homogeneity of variance). Hence, a non-parametric test (Kruskall-Wallis) was required in the analysis.

2. Biomass values have been converted to $g\ m^{-2}$ from $g\ quadrat^{-1}$ and $g\ core^{-1}$ by dividing the latter by conversion factors of 0.06250 and 0.01227, respectively.

Table 16. Scirpus americanus stem density, mean stem length, and maximum stem length (live stems only; $\bar{x}$ ±SE) by transect, Fraser Estuary 1987. All data were collected from non-random quadrats (see text).

Survey	1	2	3	4	5	6	7
Period (m/d)	05/13-05/19	05/25-05/27	06/08-06/10	06/22-06/24	07/07-07/09	07/21-07/23	08/05-08/07
Sample Size	16	8	8	8	8	8	16
Stem Density (no. stems quadrat^{-1}):							
Reifel Refuge	32.9±4.4	38.8±7.1	43.9±6.3	53.0±8.0	51.8±6.6	50.3±6.8	50.8±4.8
Lulu Island	49.8±3.9	61.1±7.2	67.1±10.4	74.5±9.9	79.1±9.3	75.9±7.5	73.3±4.6
Brunswick Point	68.9±11.0	84.5±19.7	88.3±20.5	95.3±18.8	92.6±18.6	85.9±14.2	78.6±10.2
Mean Stem Length (cm):							
Reifel Refuge	7.9±0.5	16.1±1.0	32.0±1.6	50.3±3.1	71.4±3.3	72.9±2.4	83.5±2.7
Lulu Island	6.6±0.4	11.7±1.1	18.4±1.8	28.8±1.9	35.6±2.3	47.2±3.2	45.6±1.7
Brunswick Point	17.2±0.9	26.7±1.8	41.6±2.4	56.5±4.3	58.9±4.5	62.3±3.5	63.1±2.7
Maximum Stem Length (cm):							
Reifel Refuge	13.1±0.5	24.9±1.3	52.1±2.9	76.3±3.2	110.3±2.6	119.3±4.8	123.1±2.6
Lulu Island	10.3±0.4	20.8±1.3	39.5±7.9	44.0±2.5	61.9±3.7	67.5±3.3	70.1±1.9
Brunswick Point	31.1±1.8	46.5±3.1	67.1±3.1	82.0±5.0	92.9±3.6	95.5±5.1	96.1±3.7

Table 17. Highest stem density, mean stem length, and maximum stem length values recorded for Scirpus americanus by transect, Fraser Estuary 1987. ($\bar{x}\pm$SE of five highest values (maximum value in brackets); n=16 for surveys 1 and 7; n=24 for surveys 2 through 6).

Survey	Reifel Refuge	Lulu Island	Brunswick Point
Stem Density (no. stems quadrat^{-1}):			
1	52±6 (73)	68±4 (82)	99±25 (158)
2	76±16 (141)	83±4 (98)	72±12 (109)
3	66±4 (79)	88±3 (95)	94±21 (155)
4	92±17 (153)	91±9 (117)	109±11 (141)
5	98±13 (144)	115±6 (136)	153±9 (171)
6	88±13 (120)	96±4 (111)	118±7 (144)
7	63±5 (75)	67±5 (76)	76±8 (90)
Mean Stem Length (cm):			
1	11.6±0.9 (13.6)	8.8±0.2 (9.6)	19.5±1.5 (23.8)
2	20.5±0.5 (22.3)	17.6±1.0 (19.8)	27.0±1.1 (31.4)
3	39.2±0.7 (40.6)	23.0±1.1 (27.2)	40.9±2.7 (49.6)
4	63.2±1.7 (68.0)	36.1±1.1 (38.7)	60.1±3.7 (72.8)
5	83.2±1.4 (87.0)	48.1±2.8 (56.5)	69.3±2.2 (74.2)
6	89.9±1.0 (91.8)	53.5±0.7 (55.3)	70.6±3.1 (81.8)
7	88.9±2.5 (97.2)	53.5±1.7 (59.5)	63.6±2.6 (73.4)
Maximum Stem Length (cm):			
1	16.4±0.5 (18)	14.0±0.8 (16)	34.8±2.1 (40)
2	35.0±1.5 (41)	29.0±1.3 (34)	50.2±0.9 (52)
3	64.8±1.4 (70)	44.4±4.9 (64)	74.6±1.9 (81)
4	90.2±1.8 (95)	52.6±0.7 (55)	90.4±1.9 (94)
5	129.4±3.4 (141)	76.0±1.5 (81)	106.4±2.3 (112)
6	124.8±2.5 (134)	83.8±1.9 (91)	104.2±6.3 (127)
7	131.8±3.4 (141)	75.6±2.1 (82)	98.0±1.8 (101)

Table 18. Summary of highest values recorded for selected Scirpus americanus growth indices by transect during survey 7, Fraser Estuary 1987. ($\bar{x}\pm SE$ of five highest values (maximum value in brackets); n=16 per transect). Aboveground indices are for live stems only.

Survey	Reifel Refuge	Lulu Island	Brunswick Point
Stem Density (no. stems quadrat^{-1})	62.6±4.6(75)	67.4±4.5(76)	76.4±8.1(90)
Mean Stem Length (total) (cm)	88.9±2.5(97.2)	53.5±1.7(59.5)	63.6±2.6(73.4)
Maximum Stem Length (total) (cm)	131.8±3.4(141.0)	75.6±2.1(82.0)	98.0±1.8(101)
Mean Stem Basal Diameter (mm)	4.8±0.1(5.0)	3.6±0.2(4.2)	4.0±0.1(4.1)
Stem Biomass (g quadrat^{-1})	26.854±2.571(34.682)	13.077±0.384(13.947)	21.327±3.718(33.295)
Mean Stem Biomass (g)	0.495±0.011(0.538)	0.265±0.030(0.378)	0.318±0.024(0.383)
Rhizome Biomass (live) (g core^{-1})	4.802±0.317(5.613)	4.037±0.663(6.530)	5.750±1.359(10.405)
Root Biomass (g core^{-1})	12.785±0.725(15.475)	15.709±1.179(19.937)	8.616±1.149(12.306)

Table 19. Correlations between Scirpus americanus growth indices during survey 7, Fraser Estuary 1987. (Pearson correlation coefficient; probability; n=48 for all indices).

	BASEDIAM	LSTEMLEN	DSTEMLEN	TSTEMLEN	MXLSTLEN	MXTSTLEN	LSTLEN3	TSTLEN2
NUMSTEMS	.0202 P= .446	.2406 P= .050	.5792 P= .000	.4557 P= .001	.4418 P= .001	.4609 P= .000	.2042 P= .082	.4147 P= .002
BASEDIAM		.7917 P= .000	.2515 P= .042	.7379 P= .000	.6791 P= .000	.6827 P= .000	.6306 P= .000	.6310 P= .000
LSTEMLEN			.2356 P= .054	.8942 P= .000	.8888 P= .000	.8308 P= .000	.9321 P= .000	.8666 P= .000
DSTEMLEN				.6457 P= .000	.5647 P= .000	.6850 P= .000	.1786 P= .112	.6225 P= .000
TSTEMLEN					.9586 P= .000	.9683 P= .000	.8147 P= .000	.9677 P= .000
MXLSTLEN						.9546 P= .000	.8399 P= .000	.9601 P= .000
MXTSTLEN							.7660 P= .000	.9457 P= .000
LSTLEN3								.8631 P= .000

LEGEND:
NUMSTEMS: NUMBER OF STEMS PER QUADRAT (LIVE STEMS)
BASEDIAM: MEAN STEM BASAL DIAMETER (LIVE STEMS)
LSTEMLEN: MEAN STEM LENGTH (LIVE PORTION)
DSTEMLEN: MEAN STEM LENGTH (DEAD PORTION)
TSTEMLEN: MEAN TOTAL STEM LENGTH (LIVE PLUS DEAD PORTIONS)
MXLSTLEN: MAXIMUM STEM LENGTH (LIVE PORTION)
MXTSTLEN: MAXIMUM TOTAL STEM LENGTH (LIVE PLUS DEAD PORTIONS)
LSTLEN3: MEAN STEM LENGTH (LIVE PORTION) CUBED
TSTLEN2: MEAN TOTAL STEM LENGTH (LIVE PLUS DEAD PORTIONS) SQUARED

Table 20. Correlations between Scirpus americanus aboveground biomass values and growth indices during survey 7, Fraser Estuary 1987. (Pearson correlation coefficient; probability; n=48 for all indices).

	DSTEMWT	TSTEMWT	MNLSTWT	MNTSTWT	NUMSTEMS	BASEDIAM	LSTEMLEN	DSTEMLEN	TSTEMLEN	MXLSTLEN	MXTSTLEN	LSTLEN3	TSTLEN2
LSTEMWT	.7202	.9971	.5453	.5458	.8240	.2880	.6248	.5058	.7241	.7473	.7034	.6429	.7482
	P= .000	P= .000	P= .000	P= .000	P= .000	P= .024	P= .000	P= .000	P= .000	P= .000	P= .000	P= .000	P= .000
DSTEMWT		.7710	.2741	.3515	.6689	.1709	.3420	.4722	.4864	.4672	.4778	.3450	.4859
		P= .000	P= .030	P= .007	P= .000	P= .123	P= .009	P= .000	P= .000	P= .000	P= .000	P= .008	P= .000
TSTEMWT			.5307	.5396	.8299	.2832	.6112	.5162	.7181	.7373	.6982	.6280	.7402
			P= .000	P= .000	P= .000	P= .026	P= .000	P= .000	P= .000	P= .000	P= .000	P= .000	P= .000
MNLSTWT				.9873	.1494	.8191	.9367	.2651	.8581	.8684	.8263	.8937	.8503
				P= .000	P= .155	P= .000	P= .000	P= .034	P= .000	P= .000	P= .000	P= .000	P= .000
MNTSTWT					.1431	.8335	.9337	.2776	.8615	.8617	.8240	.8818	.8489
					P= .166	P= .000	P= .000	P= .028	P= .000	P= .000	P= .000	P= .000	P= .000

LEGEND:

LSTEMWT: STEM BIOMASS PER QUADRAT (LIVE STEMS)
DSTEMWT: STEM BIOMASS PER QUADRAT (DEAD STEMS)
TSTEMWT: STEM BIOMASS PER QUADRAT (LIVE PLUS DEAD STEMS)
MNLSTWT: MEAN LIVE STEM BIOMASS (LIVE STEMS)
MNTSTWT: MEAN TOTAL STEM BIOMASS (LIVE PLUS DEAD STEMS)
NUMSTEMS: NUMBER OF STEMS PER QUADRAT (LIVE STEMS)
BASEDIAM: MEAN STEM BASAL DIAMETER (LIVE STEMS)

LSTEMLEN: MEAN STEM LENGTH (LIVE PORTION)
DSTEMLEN: MEAN STEM LENGTH (DEAD PORTION)
TSTEMLEN: MEAN TOTAL STEM LENGTH (LIVE PLUS DEAD PORTIONS)
MXLSTLEN: MAXIMUM STEM LENGTH (LIVE PORTION)
MXTSTLEN: MAXIMUM TOTAL STEM LENGTH (LIVE PLUS DEAD PORTIONS)
LSTLEN3: MEAN STEM LENGTH (LIVE PORTION) CUBED
TSTLEN2: MEAN TOTAL STEM LENGTH (LIVE PLUS DEAD PORTIONS) SQUARED

Table 21. Multiple regression analysis results of Scirpus americanus aboveground biomass against growth indices, Fraser Estuary 1987. (survey 7; n=16 per transect; n=48 for the entire estuary).

Dependent Variable	Independent Variable(s) (Regression Equation)	R^2	F ratio	Prob.	Residual Standard Error
1. Live Stem Biomass (g quadrat^{-1}) at:					
Reifel Refuge	-33.143+0.457(Stem Density)+0.263 (Mean Stem Length(live portion)) +4.014(Basal Diameter)	0.981	209.38	<0.0001	1.420
Lulu Island	-6.322+0.179(Stem Density)+0.147 (Mean Stem Length (total))	0.949	120.35	<0.0001	1.088
Brunswick Point	-0.114+0.270(Stem Density)+0.000086 (Mean Stem Length(live portion))^3 -0.00203(Mean Stem Length(total))^2	0.976	164.25	<0.0001	1.782
Fraser Estuary (pooled data)	-3.018+0.245(Stem Density)+0.000052 (Mean Stem Length(live portion))^3	0.914	239.24	<0.0001	2.682
2. Total (live plus dead) Stem Biomass (g quadrat^{-1}) at:					
Reifel Refuge	-37.125+0.504(Stem Density)+0.258 (Mean Stem Length(live portion)) +4.849(Basal Diameter)	0.975	147.21	<0.0001	1.827
Lulu Island	-5.724+1.804(Stem Density)+0.142 (Mean Stem Length(total))	0.946	113.16	<0.0001	1.129
Brunswick Point	0.987+0.293(Stem Density)+0.000089 (Mean Stem Length(live portion))^3 -0.103(Maximum Stem Length(live portion))	0.987	302.63	<0.0001	1.487
Fraser Estuary (pooled data)	-3.284+0.270(Stem Density)+0.000055 (Mean Stem Length(live portion))^3	0.908	222.51	<0.0001	3.020

Table 22. Multiple regression analysis results of Scirpus americanus aboveground biomass against stem density and mean stem length (live portion; cubed), Fraser Estuary 1987. (survey 7; n=16 per transect; n=48 for the entire estuary).

Dependent Variable	Independent Variable(s) (Regression Equation)	R^2	F ratio	Prob.	Residual Standard Error
1. Live Stem Biomass (g quadrat^{-1}) at:					
Reifel Refuge	-5.480+0.377(Stem Density)+0.000037 (Mean Stem Length(live portion))^3	0.949	121.75	<0.0001	2.243
Lulu Island	-1.210+0.194(Stem Density)+0.000032 (Mean Stem Length(live portion))^3	0.933	90.80	<0.0001	1.242
Brunswick Point	-1.889+0.204(Stem Density)+0.000070 (Mean Stem Length(live portion))^3	0.964	174.14	<0.0001	2.107
Fraser Estuary (pooled data)	-3.019+0.245(Stem Density)+0.000052 (Mean Stem Length(live portion))^3	0.914	239.24	<0.0001	2.682
2. Total (live plus dead) Stem Biomass (g quadrat^{-1}) at:					
Reifel Refuge	-5.861+0.409(Stem Density)+0.000038 (Mean Stem Length(live portion))^3	0.936	95.37	<0.0001	2.727
Lulu Island	0.759+0.181(Stem Density)	0.905	133.59	<0.0001	1.438
Brunswick Point	-1.993+0.243(Stem Density)+0.000072 (Mean Stem Length(live portion))^3	0.976	265.69	<0.0001	1.933
Fraser Estuary (pooled data)	-3.284+0.270(Stem Density)+0.000055 (Mean Stem Length(live portion))^3	0.908	222.51	<0.0001	3.020

Table 23. Multiple regression analysis results of Scirpus americanus mean stem biomass against growth indices, Fraser Estuary 1987. (survey 7; n=16 per transect; n=48 for the entire estuary).

Dependent Variable	Independent Variable(s) (Regression Equation)	R^2	F ratio	Prob.	Residual Standard Error
1. Mean Live Stem Biomass (g) at:					
Reifel Refuge	-0.311+0.006(Mean Stem Length)live portion))+0.090(Basal Diameter)	0.851	37.23	<0.0001	0.036
Lulu Island	-0.042+0.000002(Mean Stem Length(live portion))^3+0.050(Basal Diameter) +0.002(Mean Stem Length(dead portion))	0.989	345.93	<0.0001	0.007
Brunswick Point	0.011+0.006(Mean Stem Length (live portion))	0.874	97.24	<0.0001	0.038
Fraser Estuary (pooled data)	-0.050+0.056(Basal Diameter)+0.000001 (Mean Stem Length(live portion))^3 +0.001(Maximum Stem Length(live portion))	0.919	165.51	<0.0001	0.039
2. Mean Total (live plus dead) Stem Biomass (g) at:					
Reifel Refuge	-0.301+0.006(Mean Stem Length(live portion))+0.093(Basal Diameter)	0.798	25.61	<0.0001	0.045
Lulu Island	-0.071+0.083(Basal Diameter)+0.000001 (Mean Stem Length(live portion))^3	0.895	55.13	<0.0001	0.021
Brunswick Point	0.018+0.007(Mean Stem Length(live portion))	0.893	117.23	<0.0001	0.040
Fraser Estuary (pooled data)	-0.053+0.065(Basal Diameter)+0.000001 (Mean Stem Length(live portion))^3 +0.001(Maximum Stem Length(live portion))	0.916	159.98	<0.0001	0.041

Table 24. Multiple regression analysis results of Scirpus americanus mean stem biomass against mean stem length (live portion; cubed) and stem basal diameter, Fraser Estuary 1987. (survey 7; n=16 per transect; n=48 for the entire estuary).

Dependent Variable	Independent Variable(s) (Regression Equation)	R^2	F ratio	Prob.	Residual Standard Error
1. Mean Live Stem Biomass (g) at:					
Reifel Refuge	-0.105+0.000001(Mean Stem Length(live portion))^3+0.097(Basal Diameter)	0.801	26.08	<0.0001	0.042
Lulu Island	-0.012+0.000002(Mean Stem Length(live portion))^3+0.053(Basal Diameter)	0.969	205.38	<0.0001	0.011
Brunswick Point	0.021+0.000001(Mean Stem Length(live portion))^3+0.037(Basal Diameter)	0.891	52.93	<0.0001	0.037
Fraser Estuary (pooled data)	-0.035+0.000001(Mean Stem Length(live portion))^3+0.064(Basal Diameter)	0.907	219.69	<0.0001	0.041
2. Mean Total (live plus dead stems) Stem Biomass (g) at:					
Reifel Refuge	-0.094+0.000001(Mean Stem Length(live portion))^3+0.100(Basal Diameter)	0.748	19.32	0.0001	0.050
Lulu Island	-0.071+0.000001(Mean Stem Length(live portion))^3+0.083(Basal Diameter)	0.895	55.13	<0.0001	0.021
Brunswick Point	0.018+0.000001 (Mean Stem Length(live portion))^3+0.047(Basal Diameter)	0.886	50.61	<0.0001	0.042
Fraser Estuary (pooled data)	-0.037+0.000001(Mean Stem Length(live portion))^3+0.073(Basal Diameter)	0.906	215.47	<0.0001	0.043

Table 25. Correlations between Scirpus americanus belowground biomass values and growth indices during survey 7, Fraser Estuary 1987. (Pearson correlation coefficient; probability; n=48 for all indices).

	RHIZDEAD	ROOTS	MISC	RHIZTOT	RZRTTOT	BELOWTOT	NUMSTEMS	BASEDIAM	LSTEMLEN	DSTEMLEN	TSTEMLEN	MXLSTLEN	MXTSTLEN	LSTLEN3	TSTLEN2
RHIZLIVE	-.0846 P= .248	.4423 P= .001	.4685 P= .000	.9939 P= .000	.6954 P= .000	.6991 P= .000	.8754 P= .000	-.0179 P= .452	.1632 P= .134	.6872 P= .000	.4447 P= .001	.4393 P= .001	.4751 P= .000	.1599 P= .139	.4273 P= .001
RHIZDEAD		.4104 .002	-.0189 P= .449	.0255 P= .432	.3286 P= .011	.3164 P= .014	-.0425 P= .387	-.2122 P= .074	-.2405 P= .050	-.1477 P= .158	-.2572 P= .039	-.2368 P= .053	-.2369 P= .052	-.2937 P= .021	-.2997 P= .019
ROOTS			.5098 P= .000	.4890 P= .000	.9514 P= .000	.9488 P= .000	.4947 P=. 000	-.0899 P= .272	.0784 P= .298	.3904 P= .003	.2408 P= .050	.2309 P= .057	.2421 P= .049	.0257 P= .431	.2091 P= .077
MISC				.4679 P= .000	.5622 P= .000	.6013 P= .000	.5001 P= .000	-.1065 P= .236	.0330 P= .412	.1244 P= .200	.0828 P= .288	.0978 P= .254	.0923 P= .266	.0315 P= .416	.0334 P= .411
RHIZTOT					.7339 P= .000	.7363 P= .000	.8735 P= .000	-0414 P= .390	.1372 P= .176	.6731 P= .000	.4178 P= .002	.4146 P= .002	.4505 P= .001	.1280 P= .193	.3956 P= .003
RZRTTOT						.9988 P= .000	.6937 P= .000	-.0846 P= .284	.1095 P= .229	.5417 P= .000	.3350 P= .010	.3262 P= .012	.3476 P= .008	.0652 P= .330	.3025 P= .018
BELOWTOT							.6993 P= .000	-.0879 P= .276	.1077 P= .233	.5306 P= .000	.3285 P= .011	.3208 P= .013	.3412 P= .009	.0649 P= .331	.2942 P= .021

LEGEND:

RHIZLIVE: LIVE RHIZOME BIOMASS
RHIZDEAD: DEAD RHIZOME BIOMASS
ROOTS: ROOT BIOMASS
MISC: MISCELLANEOUS PLANT BIOMASS
RHIZTOT: TOTAL RHIZOME BIOMASS (LIVE PLUS DEAD)
RZRTTOT: TOTAL RHIZOME PLUS ROOT BIOMASS
BELOWTOT: TOTAL BELOWGROUND PLANT BIOMASS
NUMSTEMS: NUMBER OF STEMS PER QUADRAT (LIVE STEMS)
BASEDIAM: MEAN STEM BASAL DIAMETER (LIVE STEMS)
LSTEMLEN: MEAN STEM LENGTH (LIVE PORTION)
DSTEMLEN: MEAN STEM LENGTH (DEAD PORTION)
TSTEMLEN: MEAN TOTAL STEM LENGTH (LIVE PLUS DEAD PORTIONS)
MXLSTLEN: MAXIMUM STEM LENGTH (LIVE PORTION)
MXTSTLEN: MAXIMUM TOTAL STEM LENGTH (LIVE PLUS DEAD PORTIONS)
LSTLEN3: MEAN STEM LENGTH (LIVE PORTION) CUBED
TSTLEN2: MEAN TOTAL STEM LENGTH (LIVE PLUS DEAD PORTIONS) SQUARED

Table 26. Multiple regression analysis results of Scirpus americanus belowground biomass against growth indices, Fraser Estuary 1987. (survey 7; n=16 per transect; n=48 for the entire estuary).

Dependent Variable	Independent Variable(s) (Regression Equation)	R^2	F ratio	Prob.	Residual Standard Error
1. Live Rhizome Biomass (g core^{-1}) at:					
Reifel Refuge	-0.486+0.081(Stem Density)	0.900	126.61	<0.0001	0.593
Lulu Island	-0.136+0.058(Stem Density)	0.725	36.85	<0.0001	0.878
Brunswick Point	-0.629+0.059(Stem Density)+0.088 (Mean Stem Length(dead portion))	0.865	41.65	<0.0001	1.148
Fraser Estuary (pooled data)	-0.824+0.058(Stem Density)+0.063 (Mean Stem Length(dead portion))	0.815	99.19	<0.0001	0.945
2. Root Biomass (g core^{-1}) at:					
Reifel Refuge	2.874+0.143(Stem Density)	0.562	17.95	0.0008	2.765
Lulu Island	10.027-0.00765(Mean Stem Length (total))^2+0.341(Maximum Stem Length(live portion))	0.542	7.68	0.0063	3.381
Brunswick Point	1.219+0.055(Stem Density)+0.127 (Mean Stem Length(dead portion))	0.749	19.38	0.0001	1.843
Fraser Estuary (pooled data)	4.694+0.088(Stem Density)	0.245	14.90	0.0004	4.150
3. Total Belowground Biomass (g core^{-1}) at:					
Reifel Refuge	2.579+0.232(Stem Density)	0.749	41.79	<0.0001	2.947
Lulu Island	No variables entered	-	-	-	-
Brunswick Point	0.934+0.121(Stem Density)+0.219 (Mean Stem Length(dead portion))	0.856	38.55	<0.0001	2.610
Fraser Estuary (pooled data)	4.949+0.166(Stem Density)	0.489	44.01	<0.0001	4.537

Table 27. Multiple regression analysis results of Scirpus americanus belowground biomass against stem density, Fraser Estuary 1987. (survey 7; n=16 per transect; n=48 for the entire estuary).

Dependent Variable	Independent Variable(s) (Regression Equation)	R^2	F ratio	Prob.	Residual Standard Error
1. Live Rhizome Biomass (g core^{-1}) at:					
Reifel Refuge	-0.486+0.081(Stem Density)	0.900	126.61	<0.0001	0.593
Lulu Island	-0.136+0.058(Stem Density)	0.725	36.85	<0.0001	0.878
Brunswick Point	-0.001+0.076(Stem Density)	0.788	51.95	<0.0001	1.388
Fraser Estuary (pooled data)	-0.195+0.071(Stem Density)	0.766	150.81	<0.0001	1.050
2. Root Biomass (g core^{-1}) at:					
Reifel Refuge	2.874+0.143(Stem Density)	0.562	17.95	0.0008	2.766
Lulu Island	Not significant	-	-	-	-
Brunswick Point	2.121+0.081(Stem Density)	0.634	24.20	0.0002	2.145
Fraser Estuary (pooled data)	4.694+0.088(Stem Density)	0.245	14.90	0.0004	4.150
3. Total Belowground Biomass (g core^{-1}) at:					
Reifel Refuge	2.579+0.232(Stem Density)	0.749	41.79	<0.0001	2.947
Lulu Island	Not significant	-	-	-	-
Brunswick Point	2.490+0.165(Stem Density)	0.758	43.79	<0.0001	3.259
Fraser Estuary (pooled data)	4.949+0.166(Stem Density)	0.489	44.01	<0.0001	4.537

Table 28. Surface water salinities (ppt; $\bar{X}\pm SE(n)$) by transect, Fraser Estuary 1987.

Survey Period (m/d)	2 05/25-05/27	3 06/08-06/10	4 06/22-06/24	5 07/07-07/09	6 07/21-07/23	7 08/05-08/07
Reifel Refuge	4.6±0.6(8)[a]	0.4±0.4(24)[a]	0.0±0.0(12)[a]	0.0±0.0(3)[a]	5.8±1.6(12)[a]	2.0±0.0(12)[a]
Lulu Island	13.9±2.1(8)[b]	14.6±0.4(24)[b]	4.8±0.4(12)[b]	8.6±0.4(9)[b]	15.2±0.5(12)[b]	11.7±1.0(12)[b]
Brunswick Point	8.3±3.0(8)[a,b]	5.4±1.6(24)[c]	5.2±2.5(12)[b]	9.3±2.7(8)[b]	17.5±1.9(12)[b]	5.2±0.9(12)[c]
Fraser Estuary	8.9±1.1(24)	6.8±0.8(72)	3.3±0.6(36)	5.9±1.0(20)	12.8±1.0(36)	6.3±0.7(36)
Kruskall-Wallis H. stat.	14.75	61.29	24.57	7.80	26.21	32.49
Prob.	<0.001	<0.001	<0.001	<0.025	<0.001	<0.001

Notes:

1. Salinities were not collected during survey 1.
2. Standard errors for the Fraser Estuary were calculated by pooling all data from the 3 transects. Survey 5 was the only survey with uneven sample sizes by transect.